

CHROMOSOMES AND PLANT-BREEDING



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CHROMOSOMES AND PLANT - BREEDING

By

C. D. DARLINGTON, Ph.D., D.Sc.

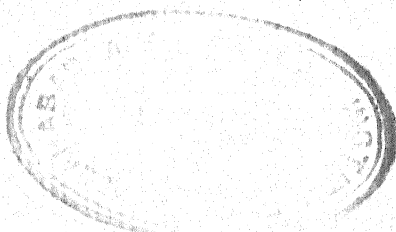
Cytologist

JOHN INNES HORTICULTURAL INSTITUTION

WITH A FOREWORD BY

SIR DANIEL HALL, K.C.B., F.R.S.

DIRECTOR OF THE JOHN INNES HORTICULTURAL INSTITUTION



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FOREWORD

THE study of genetics, which may be roughly defined as the science underlying the work of the breeders engaged upon the improvement of the races of animals and plants, for a long time advanced no further than a general appreciation of the existence of heredity—that characteristics of the parents were transmitted to their offspring. The inheritance was, however, so irregular—often, indeed, in contradiction to experiment—and the earlier surmises as to the part played by one or other sex in the constitution of the offspring were so irreducible to system, that the practical breeder could get little further guidance than the maxim that like would tend to bring like and that continuous selection, assisted by a certain amount of inbreeding, might fix the desired type.

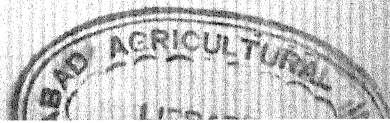
At the beginning of this century came the re-discovery of certain experiments of Gregor Mendel, published thirty-five years earlier, which contained the first statement of an exact law of inheritance. Broadly speaking, Mendel's generalisation indicated that particular characters in either parent are transmitted to the offspring as units and remain in them as units. The appearance of the character in each individual is governed by two units, one contributed by each parent; but the two units retain their identity and do not merge. The pure-breeding character is obtained only when the two units are alike; when the two units are unlike, one may be dominant and produce the outward character associated with the double unit, or the character may be inter-

mediate. Mendel's classical example was the crossing of a tall variety of pea with a dwarf variety. From one parent each seedling derives the unit carrying tallness, from the other the unit carrying dwarfness, but as in this case the tall unit is dominant, all the seedlings are tall, though they carry hybrid tallness and not pure tallness. On breeding a second generation between the hybrids, a rearrangement of the units takes place on the basis of the chance association of one unit from each pair, with the result that on the average one-quarter of the progeny will contain a pair of tall units and will be pure, one-quarter will contain a pair of dwarf units and will be pure dwarfs, and one-half will contain both kinds of unit and will reconstitute the parental hybrids. Thus is explained the segregation from mixed stocks of lines breeding true for a particular character, and again the persistence in mixed stocks of a character which may remain unseen for many generations and then suddenly reappear.

The new science of genetics then became occupied with the development of the Mendelian hypothesis on the basis of the transmission of characters by units, or genes as they came to be called, and the unravelling of the many exceptional cases that arose owing to the partial association of certain genes, whereby the simple ratios expected become distorted. The next step in the development of genetic theory was the recognition that from time to time a gene would undergo a transformation, whereby a new character might appear in plant or animal. Of late years it has been found that the frequency of these "mutations" of genes can be speeded up by the influence of X-rays upon the reproductive cells of the organism.

Then followed a remarkable interpretation of the

Mendelian hypothesis which supplied for the first time a physical basis in the structure of the organism for the generalisations that had arisen by experiment, and the theories of heredity. For a long time men of science had been engaged in the study of the structure of the cells of which all living organisms are built up, and in particular of the nucleus, which forms as it were the inner citadel of the cell. Little by little, for the investigation presented great difficulties overcome only by degrees, it became clear that at a certain stage in the growth of the cell the nucleus was resolved into a series of symmetrically disposed threads—the chromosomes, which existed in pairs. During growth the new cells were formed by the splitting of these threads into halves, and the migration of the halves of each chromosome into opposite ends of the cell, followed by a subsequent separation into two new cells, each exactly equivalent to the old. But special sexual cells were also formed in which a different type of division occurred through the selection of one element of each of the pairs of chromosomes, so that the cell participating in the act of sexual union contains only half the number of chromosomes present in the body cell. When the cell from the male parent fuses with the cell from the female in fertilisation, a nucleus with the full number of chromosomes is reconstituted, one element in each pair having been contributed by each of the parents, and this new cell is the starting-point for the new individual. It was Professor T. H. Morgan who made the next step in the investigation by the experimental demonstration of the conception that this process is the equivalent of the combinations and segregations that occur among the Mendelian unit characters. Working with *Drosophila*, a minute fruit fly that will reproduce itself within a fortnight, so that



he was able to get a rapid succession of generations, Morgan was able to demonstrate that Mendelian characters like eye colour, nervation of wings, etc., went in and out of combination in breeding experiments precisely as did certain distinguishable chromosomes. Thus the chromosomes became recognised as the carriers of heredity, and a physical basis was provided by the chromosomes for the Mendelian generalisations. Further analysis not only revealed the association of this and that gene with particular chromosomes, but also with specific fractions of that chromosome; the observed linkages can be correlated with the proximity of the fractions carrying the linked genes, and "crossing-over" occurs when the chromosomes break and change partners. The association of all the facts revealed by genetic experiments with the chromosome structure of the nucleus is now generally accepted, and the gene in the chromosome becomes the fundamental fact of biological science just as the atom is of physical science. Indeed, the revelation of the inner structure of the nucleus is not less wonderful than the contemporaneous elucidation of the atom, and, as it concerns living organisms, is even more pertinent to human beings.

It has been Dr. Darlington's purpose in the present book to set out the recent developments in the study of the chromosomes and to point out their bearing on the practice of plant-breeding. Science in these matters has been advancing at such a pace, Dr. Darlington himself contributing, and the records of investigation are scattered through so many periodicals, that all students may well be grateful to have the records of recent research gathered together and presented as a whole. Further, it has become necessary for the practical hybridist and plant-breeder, even the amateur who

aspires to take a part in the improvement of his favourite plant, to make himself acquainted with the chromosome basis of the theory of heredity. So many of the problems that force themselves upon the notice of the plant-breeder—for example, those concerning sterility and fertility—are intelligible only on the chromosome basis. Particularly, many of the curious anomalies in the behaviour and breeding of our chief fruit-bearing plants—notably apples, plums, cherries, and the raspberry and blackberry class, have only become explicable since it has been recognised that the normal nuclear group may become multiplied in an exceptional individual by the formation of a nucleus with three, four or upwards, sets of chromosomes. These individuals, called polyploids—really new species—may be fertile or sterile according to their constitution, and are often larger in all their parts and possess great somatic vigour, so that even when sterile they may be commercially valuable because they can be multiplied vegetatively. The acquisition of all this new knowledge of nuclear structure has happened to coincide at the John Innes Horticultural Institution with the coming to fruition of many of the breeding experiments on such fruit trees initiated by Mr. M. B. Crane. Consequently in the following pages the reader will find several striking examples where the results of the breeding experiments find their explanation in the nuclear structure elucidated by Dr. Darlington and his colleagues. Sometimes the theory thus reached indicates to the plant-breeder the

FOREWORD

to use Blenheim Orange or Bramley's Seedling in their crosses, unimpeachable parents on the simple "like breeds like" theory? In this book Dr. Darlington explains why such failures occur. The plant-breeder will always be engaged in a game of chance; but knowledge such as Dr. Darlington's book affords will often enable him to calculate the odds against him. It may save him from taking a ticket in a sweepstake with one prize to a million blanks, it may offer him a practical certainty if he will persevere along another line of work.

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NOTE

This book is based on a series of articles that appeared in the *Gardeners' Chronicle* (Vol. 90) in 1931. They were intended primarily for the horticulturist, but additions have been made to show the importance of chromosome studies to botanists in general. I hope the book will now provide a general introduction to the study of plant chromosomes.

C. D. DARLINGTON.

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CHAPTER I

TWO WAYS OF STUDYING HEREDITY

HEREDITY is the principle that like begets like. If this principle is examined, it is seen to mean that a particular plant or animal has certain properties resembling those of its parents, because it has grown out of certain material received from them. In the flowering plants, pollen produced in the anthers fertilises the ovules borne by the ovaries, to give the new seedling plant. The material is therefore transmitted by the pollen and the ovules.

It might seem that the most obvious way of studying heredity in plants would be by observing the structure and growth of their pollen and ovules. But the classical method of genetics—the method of Mendel, Bateson, Correns, De Vries and Morgan—has been to record and enumerate the resemblances and differences found between the parents and their more or less mature offspring. The reason for this is twofold. In the first place, these are the differences that are of importance to the cultivator and the botanist; in the second place, it is among the mature plants that countless differences, often readily classified, are to be found.

In the germ-cells, provided by the pollen and the ovules, it has only recently become possible to recognise the differences that actually occur between different races and species of plants and animals. The necessary methods have only been worked out little by little. These methods are drastic; they require the killing

and special staining of the parts of the plant to be studied. Only gradually, therefore, has it been possible to find out which of the structures seen after this treatment are important in heredity, and which are merely incidental to the treatment. Naturally, the observations of these microscopic differences have no meaning in themselves for those who are interested only in the mature plant. But when the conclusions drawn from these observations of microscopic structure are compared with the results obtained by the methods of classical genetics, they are found either to agree with them or to provide an explanation of what had proved too complicated to work out and understand from the use of the classical methods.

Our object, therefore, will be to describe the conditions found when the hereditary materials are examined through the microscope in the study of cytology, and to show the bearing these conditions have on all kinds of behaviour in the growing and mature plant. The same principles apply in animals—whether mammals, insects or amœbae—and differences occur only in matters of detail.

CHAPTER II

THE CELL AND ITS NUCLEUS

IN order to find out what is important in the pollen and the egg-cell, through which a parent is connected with its offspring, we must first inquire into the processes by which they give rise to the mature plant. The microscope reveals that the plant is divided up by cellulose partitions into small units called cells. Each of these cells is similar in essentials to the first single cell of the embryo, and the whole plant is seen to arise from this single cell by its expansion or growth, and by the formation of new cell-walls or partitions across the cell. In this way, by division, one cell grows into many.

But this observation does not teach us much about heredity, because evidently heredity depends upon the *permanence* of certain of the materials handed on from one generation to another, and these cell-walls have nothing permanent about them. They are not even indispensable to the cell, for some cells have none.

When looked at more closely, every cell, including the egg-cell and the young pollen-grain, is seen to have a single constant structure, called the *nucleus*. This body may be recognised not so much by its size, shape or chemical properties, as by the special series of changes that it undergoes at the time the cell divides. This behaviour is called "mitosis," and it is now known that all nuclei in plants and animals arise by mitosis or

some modification of it; and that they always arise from pre-existing nuclei, just as all cells arise from pre-existing cells and all plants from pre-existing plants. It is in this "division" by mitosis, therefore, that the permanent structures of importance in heredity must be sought.

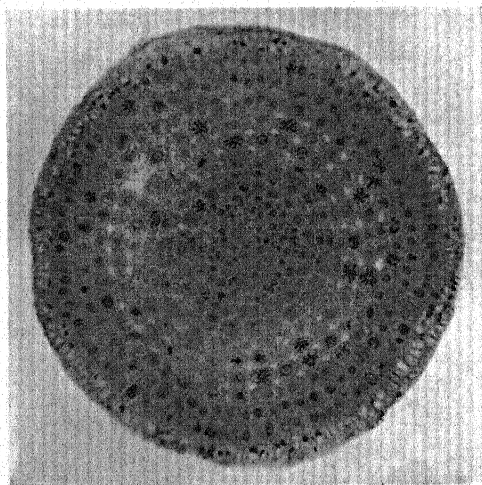
CHAPTER III

MITOSIS

THE nucleus during the resting stage is usually spherical. It lies embedded in the so-called "living" material of the cell, the "cytoplasm"—a relatively homogeneous, structureless, semi-fluid material. The finer structure of the nucleus is destroyed by the reagents used to prepare vegetable tissues for microscopic examination, but in the living cell it appears to be homogeneous. Its later changes show it to consist of a thread, or, rather, a number of threads, closely coiled together, very much like a ball of wool. When seen in section, the nucleus has a net-like appearance. Apart from this coil, the only other structures in the nucleus are certain viscous, spherical bodies called the "nucleoli" (Fig. 2), which are variable both in size and number. They have no permanence, constancy nor even, so far as anyone has been able to show, have they any use. The nucleoli may well consist of cytoplasm caught up in the nucleus as it passes into its coiled stage and temporarily dried up by contact with the coiled thread. When the thread gives up water, as it does at the onset of division, the nucleoli gradually disappear.

At this stage, the "prophase," the threads, losing water, become more viscous; and when the plant is killed and stained with suitable dyes, they are strong enough to resist the treatment. Then for the first time their structure may be seen. It is thus discovered that

in any particular plant the threads are constant in form, size and number (Fig. 1). They are double throughout their length, and each half has the appearance of a series of unequal beads unequally strung. *But the two halves are always identical.* These double threads are the chromosomes (Fig. 2, c). The doubleness is the result of their



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FIG. 1.—MITOSIS: PHOTOGRAPH OF A SECTION THROUGH A ROOT TIP OF *CREPIS DIOSCORIDIS*.

Eight chromosomes appear constantly in all the nuclei when they divide, and these can be seen to be of four constant types. In cells in which the chromosomes cannot be seen the nuclei are in the resting stage.

having split into halves along their whole length during the resting stage; but it is usual to speak of their "division" as occurring when they separate to the two daughter nuclei. Before doing this, the chromosomes contract, as a rule to less than one-tenth of the length they had during the resting stage, and they do this by each half coiling itself into a tight spiral, so that each contracted chromosome consists of two

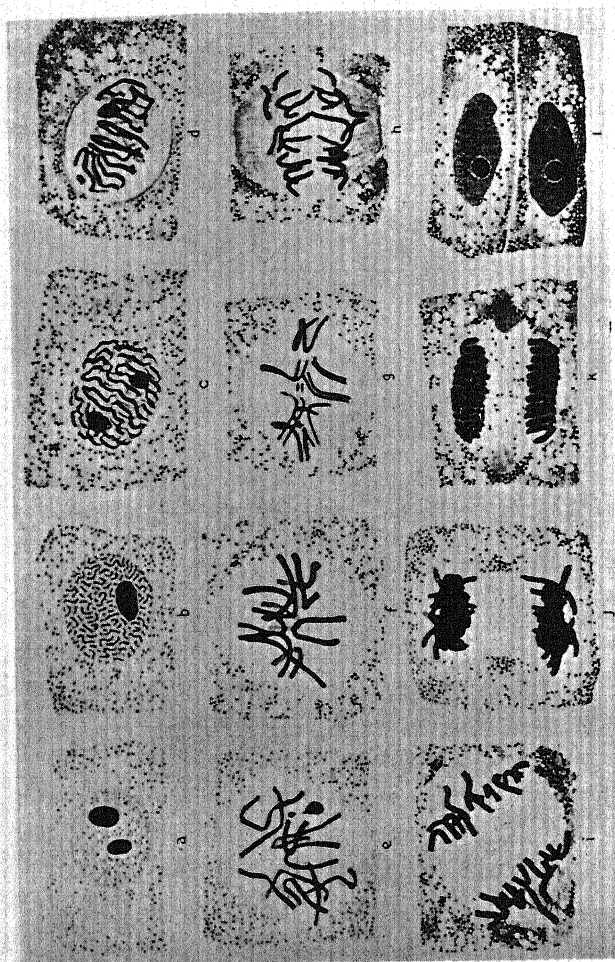


FIG. 2.—MITOSIS: THE CHANGES IN THE NUCLEUS.

Successive stages of mitosis in the root-tip of the onion, *Allium Cepa*, magnified 1630 times. *a*, resting stage; *b-d*, prophase; *e*, early metaphase; *f* and *g*, metaphase; *h* and *i*, anaphase; *j-l*, telophase. The complete chromosome complement is not shown in all cells. (After Belaf, *Die Cytologischen Grundlagen der Vererbung*, 1928.)

sausage-shaped bodies lying closely side by side—so closely that each chromosome appears single except at a high magnification. When contraction is complete, the double bodies come to lie as though on a plate across the cell, and it is then, at the stage called metaphase, that it is easiest to study the whole set of chromosomes of which the nucleus is made up.

The illustration (Fig. 1) shows several cells, in a root tip of a hawkweed, with their chromosomes at a stage just before or just after metaphase, and it will be seen that although their arrangement on the plate is accidentally variable, *the number, size and shape of the chromosomes are constant*. Their shape depends on the "points of attachment" at which the two halves of each chromosome are connected with opposite poles or ends of the cell. At the point of attachment there is always a "constriction" in the chromosome like the constriction of a wasp's waist. There may also be other secondary constrictions along the chromosomes, but whether primary or secondary, these constrictions are permanent and characteristic, and the chromosomes of any kind of plant may be recognised by the constrictions peculiar to them. This is shown in other species of hawkweed in Fig. 8.

At the next stage of division of the nucleus, which is called anaphase (Fig. 2, *b* and *i*), the two halves of each chromosome are pulled apart and the two identical sets of half-chromosomes, or "daughter chromosomes," pass to opposite poles to form two new groups. They uncoil, take up water, and each group becomes a new daughter nucleus (Fig. 2, *l*).

From these observed facts it is to be learned, first, that the nucleus consists of certain structures, the chromosomes; and secondly, that when the nucleus multiplies,

it always does so by a process in which the chromosomes, so far as can be seen, are identically reproduced. With them, as with the whole plant, like begets like,

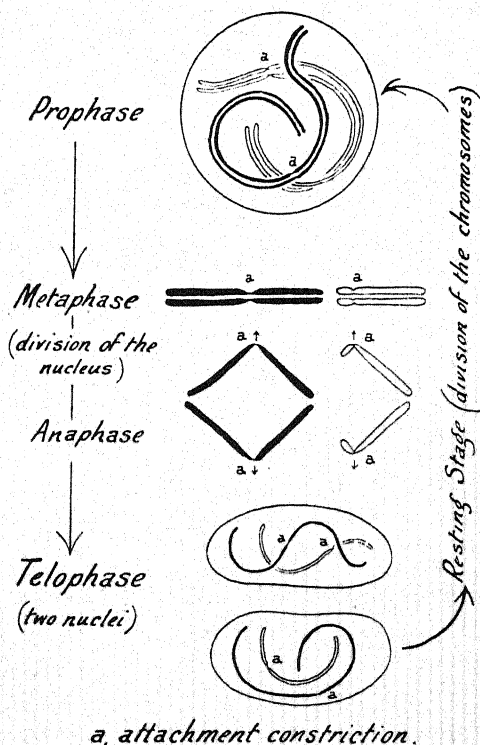


FIG. 3.—DIAGRAM OF MITOSIS.

Diagram showing the changes undergone by two chromosomes in the course of mitosis.

so that from nucleus to nucleus they propagate unchanged. Further, since all the nuclei in one plant show the same number of chromosomes at mitosis, it is evident that these chromosomes persist in the nucleus during the resting stage, although they cannot be seen. They are therefore permanent structures, and it is this

quality of permanence or constancy in the structure and arrangement of certain materials that we are looking for to account for the facts of heredity.

If this permanence is indeed characteristic of the chromosomes, it should be possible to recognise the same "complement" of chromosomes as constantly present not only in the whole of a plant (or animal), but also throughout any related group of plants—throughout a species. This is what is very generally found. In the peach there are always sixteen chromosomes, in the cabbage, eighteen, and in the tomato, twenty-four. Where there are exceptions, they are, of course, very important, but they can be traced, as will be shown presently, to special circumstances.

CHAPTER IV

CLONES : APOMIXIS

THERE are plants which have been carried on by vegetative propagation, either by bulbs, cuttings or grafts, for hundreds of years. These plants, although scattered all over the world, are all one individual from the point of view of heredity, and are called "clones." They are the results of growth with cell-division and nuclear division of the kind just described. If, then, the chromosomes are the organs of heredity, such "clones" should remain perfectly constant, for the chromosomes have divided at each mitosis into identical daughter chromosomes. This is confirmed by microscopic observation. *Tulipa Clusiana*, which is reproduced only by bulbs (for this plant is, as will be shown later, a sterile hybrid), is the same to-day in Persia or Spain or in our gardens as it was when it was illustrated in *Gerarde's Herball* (see A. D. Hall, 1929).¹ Many other species of *Tulipa*, *Fritillaria* and other genera where bulbs are the effective means of reproduction, are evidently clones and never set seed. For a like reason the apple Ribston Pippin is the same now as it was two hundred years ago, because it is propagated simply by grafting and its chromosomes have divided by mitosis at every cell-division since its origin. This applies to all fruit varieties that are carried on by grafting.

¹ *The Book of the Tulip*, London.

It very often happens that the plant carries on vegetatively without any fertilisation, *whilst appearing to reproduce from seed*. This is called apomixis, and is characteristic of many hybrid plants which rarely or never set true seed, *i.e.* seed produced as a result of the fertilisation of an egg-cell by a male generative cell from the pollen-grain. In apomixis the most usual course of development is that the tissue surrounding the embryo-sac buds and the bud produces the new embryo which forms a seed resembling the ordinary product of fertilisation. The seed produced in this way gives rise to a new plant as much like its parent as a plant grown from a cutting would be. This method of reproduction maintains the constant properties of many species of *Rubus*, *Rosa* and *Hieracium* (Rosenberg, 1930¹) which are really just as much clones as are Ribston Pippin and *Tulipa Clusiana*. These "species" of *Rosa* and *Hieracium* are by origin hybrids. It is in this way, too, that the "wild pear" of Natal, *Ochma serrulata* (a common greenhouse plant), is carried on from generation to generation, constant although by origin a hybrid (Chiarugi and Francini, 1930²). Many species of *Allium* and *Festuca* and other grasses reproduce "viviparously"; that is, they form buds in the place of flowers which are dropped, like seeds and propagate the plant. These also are clones when they are incapable of setting proper seed.

There are exceptions to this rule of constancy, however, some of which are due to changes in the chromosomes that can actually be seen. Before studying these the general properties of the chromosomes must be enquired into a little further. Other exceptions from the rule of constancy are presumably due to changes

¹ *Handbuch der Vererbungswissenschaft*, 2 (12).

² *Nuovo Giornale Bot. Ital.*, n. s., 37 (1).

which have not yet been seen, for they are inherited as Mendelian differences. Others again, like "breaking" in tulips and some kinds of variegation (e.g. in *Abutilon*), are now known to be due to disease and have nothing to do with the problems of inheritance with which we are concerned.



CHAPTER V

FERTILISATION AND HAPLOIDY

It has long been known that seed production in most flowering plants depends upon two agents—the pollen and the ovules. But it was not known how the pollen fertilised the ovule until Strasburger in 1884 showed that one of the nuclei of the pollen-grain fuses with the egg-nucleus to give the first nucleus of the embryo, a procedure identical in essentials with that already discovered in animals.

The fusion of a second nucleus from the pollen-grain with a second double nucleus from the embryo-sac, from which the nutritive endosperm tissue is derived, is an essential accompaniment of fertilisation in the flowering plants. It was discovered by Navashin and Guignard in 1899. This triple fusion need not be further considered here beyond noticing that it is evidently responsible for the exceptional triple system of inheritance of endosperm characters, studied extensively in maize. The mother plant contributes two nuclei to the endosperm, the pollen only one. The mother plant therefore has a predominant influence in the inheritance of the characters of the endosperm.

Corresponding with the observation that the characters of the offspring are derived equally from its two parents, in almost all crosses between varieties and species, is the fact that its nuclei are descended from the product of the fusion of two nuclei derived from the two parents.

These two nuclei had similar chromosomes, each having a single or "haploid" set with a chromosome number, n . This will be spoken of as the germ-cell or haploid chromosome number. Since the chromosomes are permanent, the product of the fusion of the two generative nuclei has a double or "diploid" set with a chromosome number, $2n$, which is distinguished as the somatic or diploid number. Each type of chromosome in the diploid set can be seen to be represented twice (Fig. 9). Therefore, in the absence of hybridisation, the somatic chromosome number is generally twice the germ-cell chromosome number. Where it is not twice that number, owing to hybridisation between plants having different numbers, it is still referred to as $2n$ for convenience.

Exceptions to this rule are important because they show the correctness of our reasoning. Occasionally, fusion of pollen nucleus and egg-cell nucleus does not take place; and then one of the cells with a haploid nucleus may develop into a new embryo. The embryo then has characters derived from only one parent, and it has only one set of chromosomes. It is a "haploid" plant. This abnormality is called parthenogenesis, of which the cases recorded in the accompanying table are known in plants: fourteen with development from the female nucleus, two with development from the male.

It is evident from these cases that parthenogenesis has been found to occur occasionally wherever in flowering plants the chromosome numbers have been extensively studied, but particularly in hybridisation experiments where the embryo is stimulated by the growth of pollen which is nevertheless unable to fertilise it.

CASES OF PARTHENOGENESIS.

A.—FEMALE PARTHENOGENESIS.

Species of Parent.	Chromosome Nos.		Ostensible Male Parent.	Author.
	Parent.	Offspring.		
<i>Datura Stramonium</i> .	24	12	Self (low temperature) or <i>D. ferox</i>	Blakeslee et al., 1922 (<i>Sci.</i> , 55 , 646-7).
<i>Nicotiana Tabacum</i> .	48	24	<i>Nicotiana sylvestris</i> ($2n = 24$)	Clausen and Mann, 1924 (<i>Proc. Nat. Acad. Sci.</i> , 10 , 121-4).
<i>Triticum compactum</i> .	42	21	<i>Aegilops cylindrica</i> ($2n = 28$)	Gaines and Aase, 1926 (<i>Amer. J. Bot.</i> , 13 , 373-85).
<i>Campanula persicifolia</i> , 4x	32	16	<i>Campanula persicifolia</i> ($2n = 16$)	Gardner, 1926 (<i>J. Genet.</i> , 16 , 341-51).
<i>Oenothera Lamarckiana gigas</i>	28	14	Self	Håkansson, 1926 (<i>Hereditas</i> , 11 , 129-81).
<i>Crepis capillaris</i> .	6	3	<i>C. tectorum</i> ($2n = 8$)	Hollingshead, 1928 (<i>Amer. Nat.</i> , 62 , 282-84).
<i>Solanum nigrum</i> .	72	36	<i>S. luteum</i> ($2n = 48$)	Jørgensen, 1928 (<i>J. Genet.</i> , 18 , 133-210).
<i>Matthiola incana</i> .	14 + 1	7 + 1	Self (plant with extra small chromosome)	Lesley and Frost, 1928 (<i>Amer. Nat.</i> , 62 , 22-33).
<i>Solanum Lycopersicum</i>	24	12	Self	Lindstrom, 1929 (<i>J. Hered.</i> , 20 , 20-3).
<i>Nicotiana glutinosa</i> .	24	12	Self	Goodspeed and Avery, 1929 (<i>Proc. Nat. Acad. Sci.</i> , 15 , 502-4).
<i>Oenothera franciscana</i>	14	7	Self	Davis and Kulkarni, 1930 (<i>J. Genet.</i> , 15 , 55-80).
<i>Oenothera franciscana</i>	14	7	<i>O. franciscana sulphurea</i> ($2n = 14$)	Emerson, 1929 (<i>La Cellule</i> , 39 , 159-65).
<i>Oenothera rubricalyx</i> .	14	7	<i>O. erianis</i> ($2n = 14$)	Gates and Goodwin, 1930 (<i>J. Genet.</i> , 23 , 133-56).
<i>Digitalis mertonensis</i> .	112	56	<i>D. ambigua</i> ($2n = 56$)	Buxton and Darlington, 1931 (<i>Nature</i> , 127 , 94).

B.—MALE PARTHENOGENESIS.

Species of Parent.	Chromosome Nos.		Ostensible Female Parent.	Author.
	Parent.	Offspring.		
<i>Nicotiana Langsdorffii</i> .	18	9	<i>N. Tabacum</i> ($2n = 72$)	Kostoff, 1929 (<i>Z. f. Zellforsch.</i> , 9 , 640-2).
<i>Nicotiana Tabacum</i> .	48	24	<i>N. Tabacum</i> × <i>N. glutinosa</i> ($2n = 72$)	Clausen and Lammerts, 1929 (<i>Amer. Nat.</i> , 63 , 279-82).

Haploid plants are often as healthy and long-lived as their parents, but are never more than half the size in all their parts. They are, as a rule, entirely sterile; neither anthers nor fruits are even proportionately developed, and seed formation is exceptional. In the case of the haploid tomato (illustrated in Fig. 11), the pollen was useless on sixty other varieties as well as on its parent; but when pollen of other varieties was used on the haploid, forty-two seedlings were raised by Lindstrom. These were the whole of the progeny of nearly one hundred fruits, so that the seed fertility was not much more than one per cent. of what is possible in the diploid. The reason for this sterility will be seen later. All the seedlings raised from this and other haploids are diploid, or approximately so, with the normal diploid properties.

While these haploids are of no importance for cultivation, their occurrence illustrates in the simplest way the kind of irregularity that may take place, particularly where hybridisation is being carried out, in the development of the embryo, and the important part that irregularity in the behaviour of the nucleus plays in the life of the plant.

It may be mentioned in passing that in some animals parthenogenesis giving haploids is an essential part of the reproduction of the species. Thus the female bee (queen or worker) is diploid, but the male (drone) is haploid. His haploidy and maleness are the result of his having arisen from a haploid egg which the queen laid without allowing the spermatid fluid, which she carries after mating, to escape on to it.

CHAPTER VI

REDUCTION OR MEIOSIS

FERTILISATION is the essential process in the sexual reproduction by which most species of plants and animals maintain themselves. It consists in the fusion of two nuclei, *i.e.*, in the bringing together or addition of the two sets of chromosomes of the germ-cells or gametes. Since this process is repeated in successive generations without any alteration in the number of chromosomes, it is evident that to compensate for the addition some change must take place in the nuclei before the new germ cells are formed. The German zoologist, Weismann, saw that this must be so in 1887, some time before the change had been observed, and he called it "reduction."

Weismann pointed out that reduction must occur on both the male and female sides so that both kinds of germ cells shall have half the number of chromosomes of the parent and, of course, of the offspring to which they give rise. He also pointed out that this must mean a separation of the "hereditary tendencies" of the grandparents. This separation results in what is now known as Mendelian segregation—the separation of the parental characters which is normally found in crosses between dissimilar plants or animals where they are both normally diploid.

Weismann's prediction has been fully justified. Before new germ-cells can be formed the nucleus has to go

through a special sort of mitosis in which two divisions of the nucleus and of the cell follow one another rapidly, while the chromosomes only divide once. In this way each pollen mother-cell and each embryo-sac mother-cell divides to produce four cells—pollen grains or potential embryo-sacs—each with the haploid number of chromosomes. In these divisions the chromosomes obey the same rules as in two ordinary mitoses, but the first division starts *out of step* in the following way. Prophase begins, and the chromosomes become visible as single threads; they have not yet split (see Fig. 4). In an ordinary mitosis the half chromosomes lie together in pairs, as though the chromosomes were not completely divided. In reduction or *meiosis* this condition is imitated by the corresponding pairs of unsplit chromosomes, derived from the plant's parents, coming together side by side. After this pairing is complete, there are therefore the haploid or reduced number of chromosome threads instead of the diploid number as at an ordinary mitosis.

The chromosomes then split so that (for the moment) there are four threads lying closely associated. They then immediately fall apart, so that again association is only between pairs of threads. But it is now found that each pair of threads exchanges partners at one or more points with the pair with which it has been associated (see Fig. 4, end of prophase).

It might be thought that this exchange or "chiasma" as it was called by Janssens (1924)¹ was merely the result of the four half-chromosome threads pairing at random among themselves. But it is now believed to follow an exchange of segments or "crossing-over" between two of the half-chromosomes (cf. Darlington,

¹ *La Cellule*, 34.

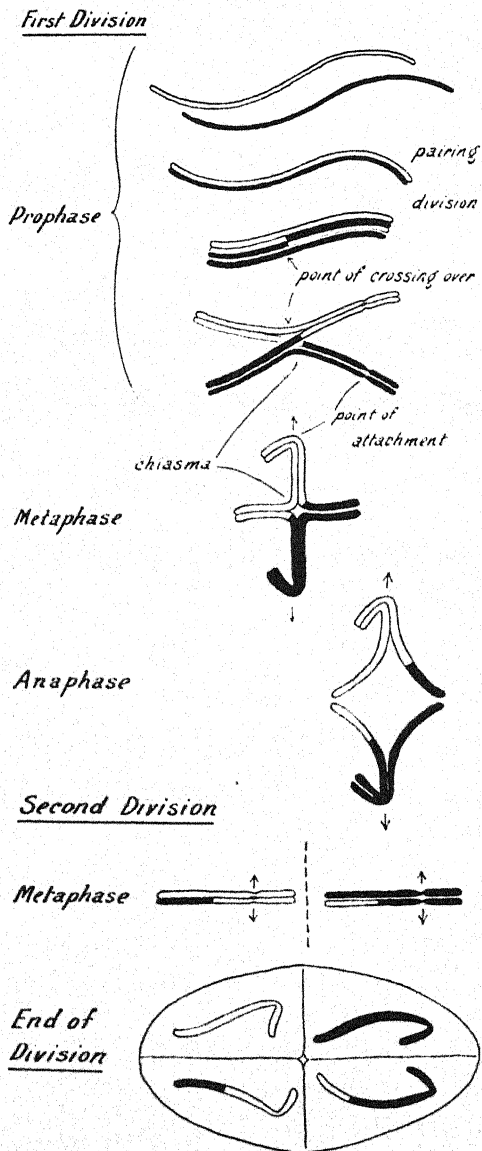


FIG. 4.—DIAGRAM OF REDUCTION OF CHROMOSOMES IN GERM-CELL FORMATION.

Crossing-over occurs at the moment the chromosome divides into two threads, and the point of the crossing-over becomes the chiasma when the chromosomes fall apart at the fourth stage of prophase. The "point of attachment" is the spindle attachment at the primary constriction.

1930¹). If the original corresponding threads are called *ABCDEF* and *abcdef*, and the exchange took place between the paired particles *Bb* and the adjoining particles *Cc*, then the four half-chromosomes following exchange will be *ABCDEF*, *ABcdef*, *abCDEF*, *abcdef*. Corresponding parts of the halves derived from splitting of the same parent chromosome remain paired, hence the observed chiasma. Two of the four half-chromosomes are different owing to the exchange. Moreover, in other cells the exchange may take place at a different point—between *C* and *D* or between *D* and *E*, so that new combinations of the chromosomes of the two parents arise in every germ-cell (Fig. 4).

This is just what is required by the breeder's observation of crossing-over or exchanging between corresponding linkage groups derived from the plant's parents. The linkage groups are groups of factors associated with one pair of chromosomes, and crossing-over is the exchange of segments between them. Such behaviour, as we shall see, is one of the conditions of Mendel's second law, viz. that different factors recombine at random in the second generation from a cross.

The chromosomes, after this falling apart or "looping" stage, continue to contract as in an ordinary mitosis, and they remain held together in pairs. This holding together depends on the exchanges caused by crossing over, for every pair has one or two of these exchanges.

When contraction is complete, the chromosomes arrange themselves in a flat plate as in an ordinary mitosis, but, owing to their pairing, the separate bodies appear in the haploid or halved number. It is then found that, as earlier, the members of each pair of

¹ *Proc. Roy. Soc., B.*, 107.

chromosomes agree in size and shape. They correspond, as indeed they must do, since the members of each pair pass to opposite poles and hence to different germ-cells without any relation to the members of the other pairs. If it were supposed that corresponding chromosomes did not pair, but that the *A* of one set paired with the *B* of another, while the *B* of the one paired with the *A* of the other, then there would be some germ-cells with two *A*'s and some with two *B*'s, and the offspring produced by them would have all kinds of combinations of different chromosomes. Actually the offspring produced in the normal way always have the same combinations of the different chromosomes, the same *complement*, as their parents. Wherever the chromosomes differ in size it can be seen that one of each type occurs in the gamete and two in the plant resulting from fertilisation.

At anaphase the paired chromosomes disentangle themselves from their exchanges. Each chromosome consists of a pair of half-chromosomes held together at their attachment points, probably because the chromosomes have not yet divided at these points; one pair passes to the one pole, while the other pair of half-chromosomes passes to the other pole. When all the chromosomes have reached the two poles, they then, being already double, separate again in a second division, and four nuclei are formed, each with the haploid number of chromosomes; *i.e.*, each with one of each kind of chromosome derived from the germ-cell of one of the plant's parents.

This is the mechanism by which the chromosome complement is "reduced" so that the new germ-cells have the same number of chromosomes and the same kinds of chromosomes as those produced by the preceding

generation. But if, as begins to be apparent, the qualities of the chromosomes underlie the qualities of the plants themselves, this reduction means that the qualities of the two parents do not blend; they separate, and in the next generation recombine and separate again. They recombine, both as between different chromosomes by their passing at random to the two poles, and as between different parts of the same pair of chromosomes by "crossing-over." This is what is meant by Mendelism, although here it has been discovered by another route.

CHAPTER VII

MENDELISM

THE Mendelian principles referred to several times already are of universal application in heredity where sexual reproduction takes place. They will now be briefly explained for those readers who are not already familiar with them.¹

The laws of inheritance discovered by Mendel may be stated in the following way. The differences of character observed between individuals of a species are determined by units of inheritance called "factors." Any plant or animal has a pair of factors affecting each variable character, one derived from the germ-cell of each of its parents; and in turn it contributes one or other of these factors to each of its germ-cells. Any individual (whether sweet pea, mouse or fly) which breeds true to a particular character, such as height or colour, has received from its parents two *identical* factors, and the germ-cells which it produces must be all of one kind in regard to the factor for this character. True-breeding plants and animals are therefore said to be "homozygous," a term derived from two Greek words implying the yoking or union of like things—the two parental germ-cells.

When the pollen of one true-breeding plant is used to fertilise the ovules of another of a different type, each of the offspring will be mixed in regard to the pair,

¹ Cf. R. C. Punnett, *Mendelism*, Macmillan.

or pairs, of factors determining the difference of type. Such a plant is said to be "heterozygous," a term implying the union of unlike things. It is produced from two sorts of germ-cells. And it likewise produces two sorts of germ-cells—in equal proportions—one sort carrying one factor, the other its alternative. If these factors are designated A and a , the offspring of the heterozygous plant from chance mating of the germ-cells in self-fertilisation will be in the proportion of one AA to two Aa to one aa . The statement that the alternative factors in a heterozygous individual separate or *segregate* (and do not blend) in the production of germ-cells is Mendel's first law of inheritance.

It is usually found that heterozygous plants and animals show the character of one of the homozygous parents and are not intermediate. This is a property of the character itself which is said to be "dominant" while its alternative is recessive.

Mendel also found that in plants that are heterozygous in regard to several factors determining distinct characters these factors segregate independently of one another. A pea heterozygous for the tall-dwarf factor and for the green-pod-white-pod factor gives as many offspring tall and white as dwarf and green. The statement that distinct factors segregate independently is called Mendel's second law.

These statements were originally put forward by Mendel as a working hypothesis. They are now recognised as laws, for one important reason: the mechanism on which the laws depend may be seen, and it is universal. That mechanism is the mechanism of chromosome reduction and fertilisation which has just been described.

Mendel imagined corresponding pairs of factors in

the plant; now, corresponding pairs of chromosomes are found in all its cells. He imagined the segregation of factors in the production of germ-cells; now, the separation of chromosomes is seen. He imagined the recombination of corresponding factors at fertilisation; the cytologist sees the two groups of corresponding chromosomes unite. Mendel's principles may therefore be regarded as laws because their mechanism is known; and even where, as will be shown later, the application of the laws is complicated or modified out of all direct recognition, nevertheless it is known that the same principles must be at work, because the same kind of mechanism is observed.

The anthers contain hundreds or even thousands of "pollen mother-cells," and each of these divides by the process of reduction into four pollen grains, any one of which can accomplish the fertilisation of one ovule. Each ovule contains a single embryo-sac mother-cell which divides in just the same way to give four daughter-cells. But only one of these daughter-cells becomes an active germ-cell, and produces the "embryo-sac"; the rest die. The pollen grain nucleus divides, always by simple mitosis, to produce a "vegetative" nucleus which dies and two "generative" nuclei. The embryo-sac nucleus usually divides, also by simple mitosis, three times to produce eight nuclei, of which one, the egg-nucleus, unites with a generative nucleus; this fusion is the fertilisation and is the beginning of the new embryo. Another two nuclei in the embryo-sac fuse together with the second generative nucleus of the pollen-grain. From this fusion the endosperm is derived.

Since segregation occurs at reduction, it follows that a plant that is in the least degree heterozygous produces germ-cells that are different from one another not merely

in the properties that they transmit to the offspring, but also in their own behaviour. It happens in this way that the pollen-grain, which has a more active and complicated life than the embryo-sac, often fails to survive when it is slightly abnormal. It is then said that certain characters are *lethal* or fatal to the pollen; the pollen will not *carry* them, although the ovules will; instances of this will be given later.

CHAPTER VIII

THE QUALITIES OF THE CHROMOSOMES

BEFORE assuming anything more about the properties of the chromosomes the evidence already available must be looked at more closely. The fact that the chromosomes pair so regularly like with like, the fact that their differences are so perfectly constant, and finally, the fact that they have a delicate, thread-like structure and always divide longitudinally to give two identical threads: all these observations point to their having different qualities not only as whole chromosomes, but also in the different particles along the length of each chromosome. They must be longitudinally differentiated.

Now it has happened in many plants that have been bred extensively and at the same time studied under the microscope, that occasional abnormalities have been found in regard to the number of chromosomes. Instead of the normal diploid number of chromosomes, one extra has been found. Such plants are said to be "trisomic," because one chromosome type is present three times instead of twice. This condition is known in the following species (among others):—

Oenothera Lamarckiana (evening primrose), Gates, 1928¹; *Matthiola incana* (stock), Frost and Mann, 1929²; *Solanum Lycopersicum* (tomato), Lesley, 1928³ (Fig. 5); *Datura Stramonium* (thorn-apple),

¹ *Bibliographia Gen.*

² *Genetics*, 13.

³ *J. Genet.*, 13.

Blakeslee, 1929¹ (Fig. 12); *Crepis capillaris* (hawk-weed) Navashin, 1928² (Fig. 7).

As in animals, where the same sort of irregularity has been found, the individual with the odd chromo-

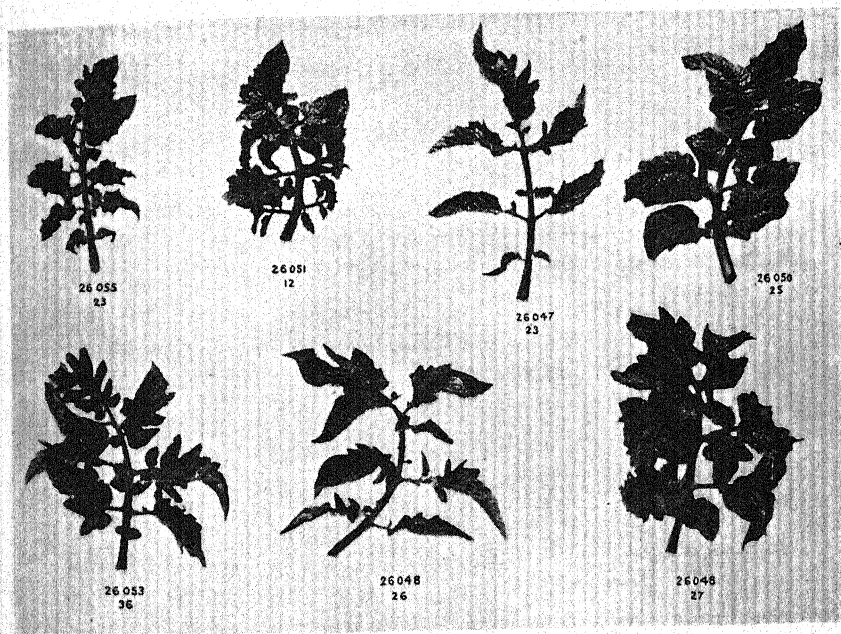


FIG. 5.—TOMATO LEAF-TYPES FOUND IN TRISOMIC INDIVIDUALS WITH DIFFERENT EXTRA CHROMOSOMES.

The normal diploid is the middle leaf in the bottom row. (From Lesley, *Genetics*, 13, 1928.)

some always has a character more or less sharply differentiated from the normal. Usually it is distinct in every organ—stem, leaf, flower and fruit. In *Datura Stramonium* it has been possible to go much further than this, and show the special effect of particular chromosomes. The thorn-apple has twelve chromosome pairs, and there have turned out to be twelve different kinds

¹ *J. Heredity*, 20.

² *Ibid.*, 15.

of plants, each with one extra chromosome. These can be recognised, *either* by looking at the plant, *or* by looking at its chromosomes.

In the tomato this kind of study is still incomplete, but already it is possible to pick out different kinds of extra chromosome types, and to say from looking at the plant which chromosome it is that is present once too often (Fig. 5).

In the stock, *Matthiola incana*, there is a particular white-flowered, double-throwing variety "Snowflake," which has the habit of giving "mutants" in this way, each with an extra whole chromosome, and there is probably one type for each of the seven chromosomes, seven being the haploid number of the stock. Snowflake usually produces from two to five per cent. of mutants, and the reason for this is found in an occasional failure of pairing of the chromosomes at reduction, probably due to the division not having started soon enough, for the chromosomes at reduction are long, like chromosomes at ordinary mitosis. The unpaired chromosomes do not necessarily pass to the opposite poles; two that would normally be paired may go to the same pole, so that germ-cells, both pollen and ovules, may be formed with one of the chromosomes present twice. Some are also formed in which one kind of chromosome is left out altogether, but since plants are never found with one chromosome too few, it is clear that nothing ever comes of these. The whole complement is necessary if the plant is to live and grow.

This habit of throwing mutants with an odd chromosome goes with the peculiarities of long chromosomes and irregular pairing at the reduction division. When the stock Snowflake is crossed with a normal plant, all the progeny are normal, and in the second generation

from the cross one quarter are like Snowflake in this habit. The character is therefore evidently a Mendelian recessive. (Lesley and Frost, 1927.¹)

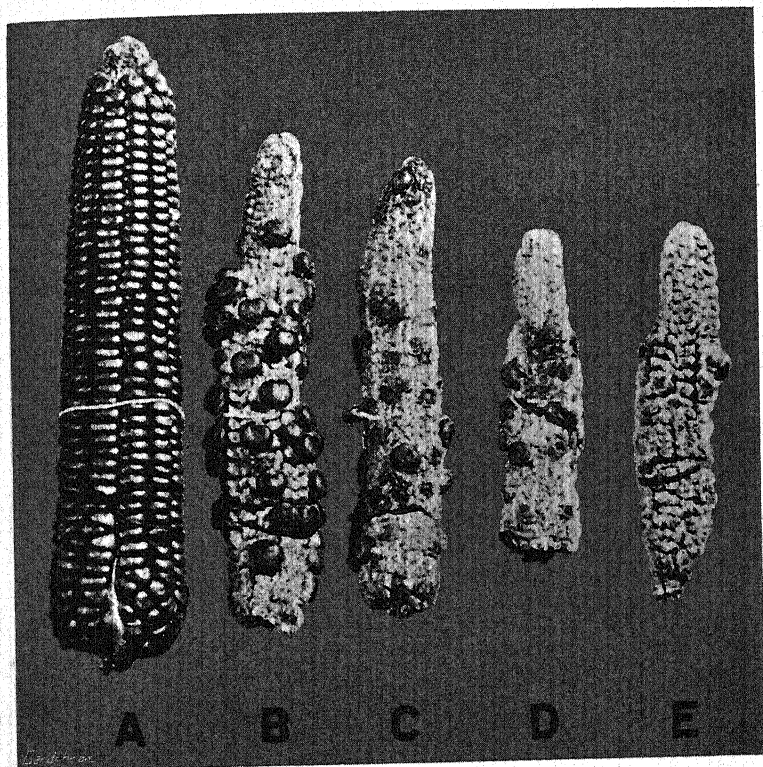


FIG. 6.—NORMAL AND DEFECTIVE MAIZE COBS.

A, Fertile maize; B, C, D, E, sterile cobs with irregular reduction. (From Beadle, 1930, *Cornell Univ. Agric. Exper. Station Memoir*, 129.)

The irregularities of reduction in this abnormal type of stock necessarily lead to a loss of fertility. This is even more strikingly seen in a parallel case in maize.² Here in the sterile form less than one-tenth of the grains

¹ *Genetics*, 12.

² Beadle, 1930, *Cornell Univ. Agric. Exper. Sta. Mem.*, 129.

develop even when fertilised with normal pollen (Fig. 6). This sterility is similarly a Mendelian recessive character, and is immediately due to a failure of normal reduction leading to the formation of germ-cells with different numbers and combinations of chromosomes.

Among other mutant types from the stock Snowflake one was found, the "small" type, with *an extra chromosome of different size* from any in the normal complement. Evidently an ordinary chromosome had broken and one of the fragments had passed as an extra chromosome to the germ cell. If the chromosome from which it was derived is named "*A*," the complement of "small" is *AAa*, *a* being a part of *A*. This kind of odd fragment has been found also in the tomato. There it is possible to tell which chromosome the fragment is derived from, for plants having this fragment have some of the peculiarities of those with the particular whole extra chromosome and these peculiarities are intensified.¹

The "small" stock mutant, like all the other trisomics, differs from the Snowflake parent in its general character. It is also of greatly reduced fertility. It produces pollen and ovules having *A*, *AA*, *Aa* and *a*, but it is found that the pollen with an extra chromosome (*AA*) or even an extra fragment (*Aa*) will not serve for fertilisation; it cannot compete with the normal *A*. Thus when a plant with one extra chromosome is self-fertilised, instead of a quarter of the progeny having two extra chromosomes of this type, only two or three per cent. of this type are formed. This kind of inheritance has been made use of in a special way, as will be seen later.

The second generation mutant with two extra chromosomes is always remarkable for an accentuation of the abnormal properties of its one-extra parent, and especially

¹ Lesley 1929, *Genetics*, 14.

in the reduction of fertility. The result is frequently a reduction in the size of the fruits, as well as a change in their shape; this is particularly well marked in *Datura*¹



FIG. 7.—A SPORT IN *CREPIS TECTORUM*.

A plant with one extra chromosome. The original plant has stunted growth (chromosomes in *b*). The tall side branch is a sport which has lost the extra chromosome and recovered the full normal size of the species (chromosomes in *a*). (From Navashin, 1930, *Univ. of Calif. Pub. in Agric. Science*, 6, 3.)

(Fig. 12). When a trisomic seedling loses its extra chromosome, it changes back to the normal appearance.

¹ Blakeslee, 1924, *Amer. Nat.*, 56.

In one case in which this has occurred in a hawkweed,¹ the result is most striking, as shown by the illustration. The normal diploid branch has arisen through an accident at mitosis in a cell at the growing point of the bud. It is much more vigorous than the trisomic branch (Fig. 7).

Abnormalities resulting from the presence of odd chromosomes are not often of direct importance in horticulture. The plant with the normal diploid number of chromosomes of the species is usually well adapted to the conditions to which the species is exposed in cultivation as well as in the wild state. It will be shown later how such changes have been of importance in the evolution of certain species, but for the present it is more important to notice the general meaning of this kind of change. It means, first, that every chromosome, and indeed every part of every chromosome (since fragments also have a special effect) has its own specific qualities, different from those of the rest. Secondly, it means that the hereditary properties of the plant are not so much the sum of all these units as their product. They depend on the *balance* between the parts of all the chromosomes. When the proportion in which one part stands to the rest is altered from two-to-two in the normal to three-to-two (where there is an extra chromosome in a trisomic plant) the whole system of the plant is altered or, rather, transformed. When the proportion is altered to four-to-two, the change is even more serious. The new types are therefore spoken of as "unbalanced." There is nothing *essentially* unfit about a plant or animal that is unbalanced, for fitness is relative to external conditions; but the plant with unbalanced chromosomes is nearly always different from the normal, and in ninety-nine cases out of a hundred the change is likely to be a change for the worse.

¹ *Crepis tectorum*, Navashin, 1930, *Univ. Calif. Pub. in Agric. Sci.*

It should be noted that loss of vigour and loss of fertility go together in these cases. There is a simple reason for this: If the odd chromosome reduces the vigour of the mature plant, it affects still more seriously the vigour of the germ-cells and their life in relation to the tissues in which they grow. At every stage of development growth is affected by a change in the balance of the chromosomes, and consequently seed fertility reduced. Seedlings raised from many of our best varieties of apples, such as Blenheim Pippin, are useless, for the reason that as they always have extra chromosomes, they are infertile and are of poor growth (Fig. 25, cf. Crane and Lawrence, 1930¹). Thus although these varieties are themselves good croppers they cannot be used for breeding. The old rule of breeding from the best cannot be applied.

The exceptions to this rule are, however, of interest. In the hyacinths, varieties occur with various numbers of chromosomes (cf. Darlington, 1929²). The normal diploid number is sixteen, but the variety Nimrod, for example, has nineteen. These varieties with extra chromosomes are not markedly less vigorous nor are they much less fertile than the older diploid varieties, and they are not readily distinguishable by their habit of growth. Similarly, in *Narcissus* and probably *Crocus* (Mather, unpublished), some of the best varieties have extra chromosomes. Evidently, in these cases, the chromosomes are less sharply differentiated from one another. We may say that each chromosome has much the same differences and much the same balance within itself as the whole set has together, for differences amongst the ultimate units there must be.

¹ *J. Genet.*, 21.

² *Ibid.*, 19.

CHAPTER IX

VARIATION

A CASE has now been made out for taking the chromosomes to be the important organs of heredity. They are permanent. They reproduce themselves exactly at each cell-division. They alone are contributed equally by both parents at fertilisation. They provide a mechanism of reduction which enables us to understand why the germ-cells of a hybrid are pure and contain material derived from only one parent in respect of characters in which the two parents differ. Finally, the chromosomes are different from one another, so that if a part of one is doubled or lost, the qualities of the whole plant are more or less sharply changed. There are then, in the chromosomes, the materials for the origin of variation. We will now see how they can be used for the study of variation and improvement in plants.

The double form of the ten-week stock, *Matthiola incana*, has been known for nearly four hundred years. It was described by Dodoens in 1568. It is absolutely sterile; both its anthers and its carpels are transformed into petals to give the showy flower that is so much valued. It arises from single stocks which are heterozygous for the double character. Normally, these therefore give, when self-pollinated, one-quarter doubles and three-quarters singles; one-third of these singles, of course, afterwards breed true to singleness while the rest throw doubles as the parent did. But there is a

particularly useful strain of "ever-sporting single" that gives seedlings half of which are single and half double; moreover, the single ones continue, like their parent, to throw half doubles and half singles. This looks like the behaviour of a back-cross, and the impression is borne out by the observation that the pollen carries only doubleness. When the ever-sporting plant is crossed on to pure singles it gives only normally heterozygous singles, and no pure singles, although both parents were heterozygous for singleness. When the pollen of the pure singles, is crossed on to it, the result is half pure singles, half normally heterozygous singles and no doubles. Evidently therefore the ever-sporting single is heterozygous for double, and produces only double pollen because its single pollen is in some way incapacitated.

Recently, a cytological study had shown how this comes about (Philp and Huskins, 1931¹). It is known that a particular pair of chromosomes is concerned with the doubling factor because when an extra chromosome of this type is present the plant gives special proportions of doubles and singles in its offspring. In the ever-sporting race it is found that a small piece or "satellite" at the end of one of this pair of chromosomes is missing. But in its double seedlings both the chromosomes are normal. Evidently, therefore, the "single"-carrying chromosome of the ever-sporting single has lost a piece and, as so often happens, the germ-cell carrying this defective chromosome is useless on the male side but effective in the ovules—owing to the life of the pollen-grain being longer and more active than that of the embryo-sac. There is never any crossing-over between the "single" factor and the lost piece. The diagram

¹ *J. Genet.*, 24.

shows how the ever-sporting race perpetuates itself (Fig. 8).

It has been found possible to combine this ever-

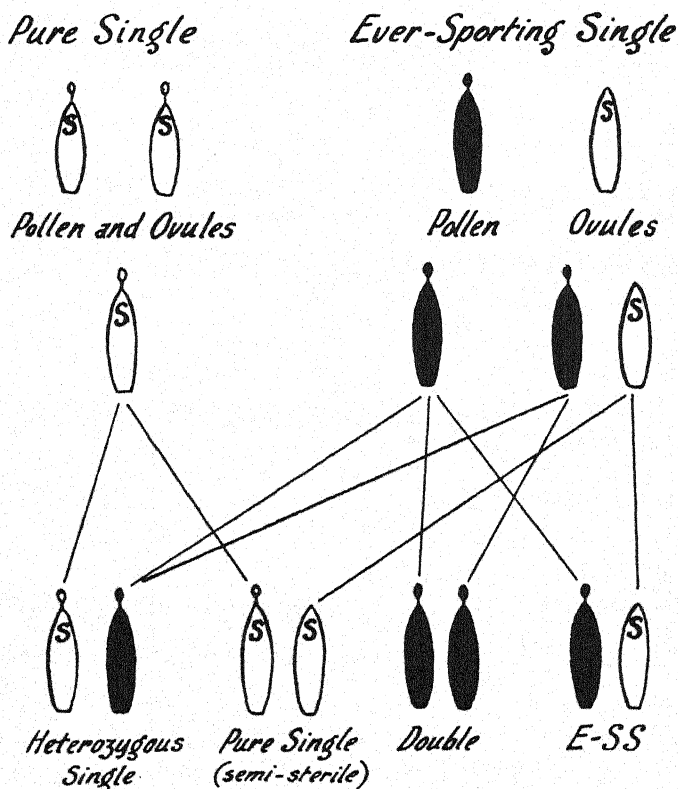


FIG. 8.—DIAGRAM TO SHOW INHERITANCE IN PURE SINGLE AND EVER-SPORTING SINGLE STOCKS.

Chromosomes carrying the double character are shown in black. Pollen-grains having chromosomes without the "satellite" do not live.

sporting mechanism with the extra chromosome mechanism described above in the case of the "small" stock to give an even more efficient means of raising double

stocks. (Frost, H. B., 1928¹.) In the progeny of Snowflake, which is an ever-sporting single variety, plants have been found with an extra fragment of the double-carrying chromosome. The presence of the extra fragment gives the plants the character of "slender." These plants are of less robust growth and can be picked out by this character in the young stage. They are nearly all single, while among the normal diploids there are eighty per cent. of doubles. By raising double stocks from the "slender" ever-sporting single strain, four-fifths of the kind wanted instead of only a half, may therefore be obtained.

There are relatively few plants yet known where, as in these cases, a particular character can be associated with the loss or gain of a piece of chromosome. Such cases are known in the fruit-fly *Drosophila*. In many horticultural varieties of the spiderwort (*Tradescantia virginiana*, Darlington, 1929²) and the Crown Imperial lily (*Fritillaria Imperialis*), and in varieties of some species of *Primula*, there are found to be fragments present in addition to the normal chromosome complement. In the absence of breeding work these cannot be associated with any particular property of the plants in question, but there is every reason to suppose that such plants have been selected for special properties associated with the fragments, since the fragments themselves reduce fertility, and are not therefore favoured in seed production.

Such changes as loss or gain of part of a chromosome, fragmentation, and the fusion of different chromosomes probably occur from time to time in all plants. The result is that we are able to see differences between

¹ "Chromosome Mutant Types in Stocks," *J. Hered.*, **19**, 105-11.

² *J. Genet.*, **21**.

the chromosome sets of different species and even between varieties. For example, in a race of the vetch *Vicia Cracca* growing in one part of Russia there are six pairs of chromosomes; in those in another part there are seven pairs, one of them being very small. Evidently the difference is due to one of the pairs

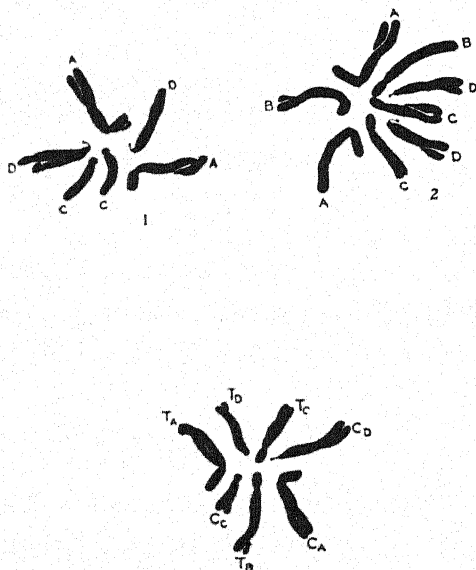


FIG. 9.—CHROMOSOMES OF *CREPIS TECTORUM* ($2n = 8$) and *CREPIS CAPILLARIS* ($2n = 6$).

The parents' chromosomes (types A-D; no B type in *C. capillaris*) can be recognised in their offspring (labelled C and T). (From Hollingshead, 1929, *University of California Pub. in Agric. Science*, 6, 2.)

of chromosomes breaking into two (Schweschnikowa, 1927¹).

Similarly in two species of the hawkweed, *Crepis*, (Fig. 10) there are differences in the shapes and sizes of the chromosomes, and one species has one pair more than the other. When these two species are crossed,

¹ *Proceedings Fifth Internat. Cong. of Genetics*, Berlin.

it is to be noticed that the chromosomes of each maintain their individuality. They can still be recognised in the hybrid as clearly as in the parent species.

When such hybrids come to form their germ-cells, it should be possible to find what the differences between their parents really amount to. Similar parts of chromosomes pair, and it will therefore be possible to tell what has happened to the different parts of the chromosomes in the interval during which the two varieties or species have been separated. If bits have been exchanged between chromosomes, or lost or gained, some abnormalities of pairing and consequently of segregation are to be expected. This is the rule in hybrids. In certain cases the abnormalities are very precise, and it is possible, as first pointed out by Belling (1927¹), to say exactly what makes the difference between the two parents. This is so in the case of geographical races of the thorn-apple, *Datura Stramonium*, and of *Campanula persicifolia*. The chromosomes in one race have evidently changed over segments at some time in their history, so that in the hybrid between two races the two ends of a chromosome from one parent pair with ends of two different chromosomes from the opposite parent, and a ring of four chromosomes appears at reduction (Blakeslee, 1929,² Gairdner and Darlington, 1931³). Such plants are best described as "interchange heterozygotes," since they are heterozygous in respect of an interchange of segments between two chromosomes.

In culinary peas (*Pisum sativum*) the same kind of interchange has been found both in crosses between different geographical races (E. R. Sansome, 1929,⁴

¹ *J. Genet.*, 18.

² "Cryptic Types in *Datura*," *J. Heredity*, 20.

³ *Genetica*, 13.

⁴ *Nature*, 124; *Cytologia*, 3.

1932) and in cultivated strains (Håkansson, 1929¹). Interchange is here of great importance to the cultivator, for it means that half the embryos are incapable of development and seed-fertility is badly impaired (Hamarlund and Håkansson, 1930²). This is because the irregular segregation of the chromosomes which are

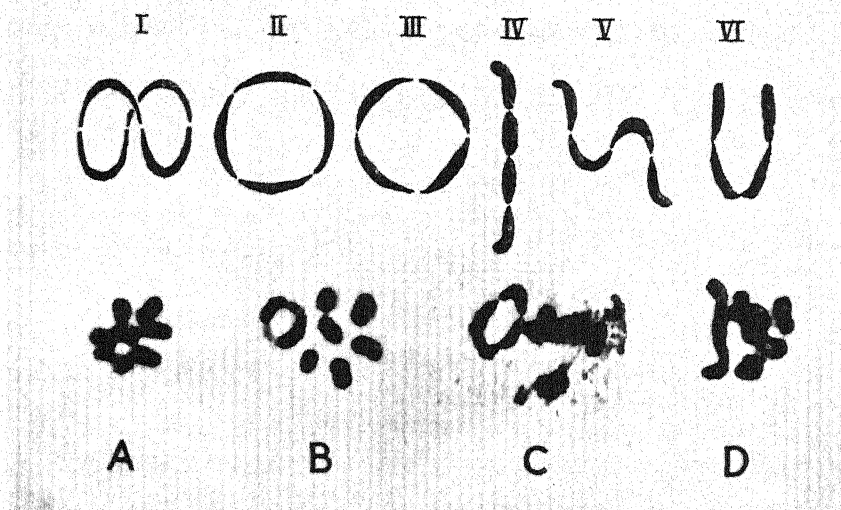


FIG. 10.—RINGS OF FOUR IN A DIPLOID PLANT.

I-VI. Diagram showing different arrangements of four chromosomes in a ring or chain at meiosis in the diploid *Campanula persicifolia* giving regular segregation in I and V only. A-D, micrographphotos. A, normal plant with eight pairs of chromosomes. B-D, a plant with four chromosomes associated. (After Gairdner and Darlington, 1930, *Nature*, 125.)

associated at meiosis in fours or sixes gives new combinations which (as in the case of plants discussed earlier, with odd chromosomes) are less likely to live than the old, normal combinations. Moreover, since the sterility depends simply on a difference in the way two pieces of chromosome are joined together, this sterility is

¹ *Hereditas*, 12.

² *Ibid.*, 14.

inherited like a single Mendelian difference, and would have been properly so described before the chromosome basis of the abnormality was discovered. Interchange heterozygotes have now been discovered in many species including *Zea Mays*, Indian corn (Burnham, 1930¹).

Such arrangements as these are frequently found in artificial hybrids, and doubtless usually arise from crossing, but sometimes these hybrid conditions are preserved even when the plant is self-fertilised. For this two conditions are necessary: First, the regular production of only two kinds of germ-cells by all the like parts of chromosomes pairing and passing to opposite poles (Fig. 10, I and V); secondly, the failure of either of these kinds of germ-cells to produce an embryo when it meets another like itself. In this way many *Oenothera* species, like *Oe. Lamarckiana*, continue hybrid from generation to generation, breeding apparently true. The only signs we get of their hybridity are these: First, that when they cross with other species they produce two kinds of hybrids—twin-hybrids—because each kind of germ-cell can live and give rise to an embryo when used in crossing. And secondly, they are constantly liable to mutate giving offspring of a new type. *Oe. Lamarckiana*, for example, gives one per cent. of forms with extra chromosomes, which, as in stocks and tomatoes, are sharply distinguished from the parent. Other mutants arise through exceptional crossing-over to which such hybrids are liable. For a fuller description of these reference must be made to a more detailed account (Darlington, 1932²).

Such a system as this can settle down to great stability.

¹ *Proc. Nat. Acad. Sci.*, 15.

² *Recent Advances in Cytology*, J. and A. Churchill.

In the hothouse succulent *Rhoeo discolor*, of which there is only one type, apart from a variegated form, all the chromosomes are joined in a ring of twelve at reduction instead of being in six pairs. But since pairing parts of chromosomes pass to opposite poles, enter different gametes, and are reunited again at fertilisation the plant breeds true, and its hybridity can only be known as yet from its chromosome behaviour. This is one of the ways in which a hybrid may breed true. Others will be met with later.

CHAPTER X

TETRAPLOIDY WITHOUT HYBRIDISATION

CELLS or groups of cells are found occasionally in mitoses of root-tips with nuclei having twice the normal number of chromosomes. These cells are bigger than their neighbours, and the root is often distorted by their presence. They are presumably the result of two nuclei failing to separate, or at least failing to have a cell-wall formed between them after a division. Naturally such an accident as this is particularly likely in the rather irregular growth of a callus, and it is from wound calluses in the tomato that whole stems have been found frequently to arise with double the diploid chromosome number of chromosomes. This method was adopted by Crane (cf. Jørgensen and Crane, 1927¹) working with the tomato and with *Solanum nigrum* to produce regularly, *i.e.*, in about six per cent. of cases, shoots with the increased chromosome number. From these, cuttings could be taken giving a new race of plant, giant in all its organs—nuclei, cells, stems, leaves and flowers; in all its organs, that is, except the chromosomes themselves (Fig. 12).

A plant with more than two sets of chromosomes is a *polyploid*. A plant with four sets instead of the ordinary two is a tetraploid. It produces germ-cells with the diploid numbers of chromosomes. In the

¹ *J. Genet.*, 8.

diploid tomato, for example, n is 12 and $2n$ is 24; in the tetraploid n is 24 and $2n$ is 48. It is convenient to refer to these higher multiples in terms of the haploid number found in the normal diploid parent. This is given the symbol x , so that in the tetraploid we can say that $2n = 4x = 48$. Tetraploid plants have been found in :—

1. *Oenothera Lamarckiana* (Gates, 1909¹).
2. *Primula sinensis* (Gregory, 1914²).
3. *Datura Stramonium* (Blakeslee and others, 1923³).
4. *Campanula persicifolia* (Gairdner, 1926⁴).
5. *Solanum nigrum* (Jørgensen, 1928⁵).
6. Various mosses (the Marchals, 1909, Wettstein, 1924⁶).

Recently tetraploid forms have also been found in *Primula malacoides* and in *Primula obconica* (Sansome, unpublished). Altogether, therefore, more than seven examples of tetraploid plants of known origin have already been discovered in experiments with pure species of flowering plants.

The oldest of these of which reliable records exist is *Campanula persicifolia*, for a form *maxima* is illustrated in Curtis's *Botanical Magazine* of 1795. It is again figured and described by Loudon in 1844, but appears subsequently to have dropped out of cultivation. From its resemblance to the tetraploid of to-day, its large, shallow bells and giant growth, it cannot be doubted that this was a tetraploid seedling of the diploid form commonly grown. Telham Beauty

¹ *Archiv. f. Zellforschung*, 3.

³ *Bot. Gaz.*, 76.

⁵ *J. Genet.*, 18.

² *Proc. Roy. Soc., B.*, 87.

⁴ *J. Genet.*, 16.

⁶ *Bibliotheca Genetica*.

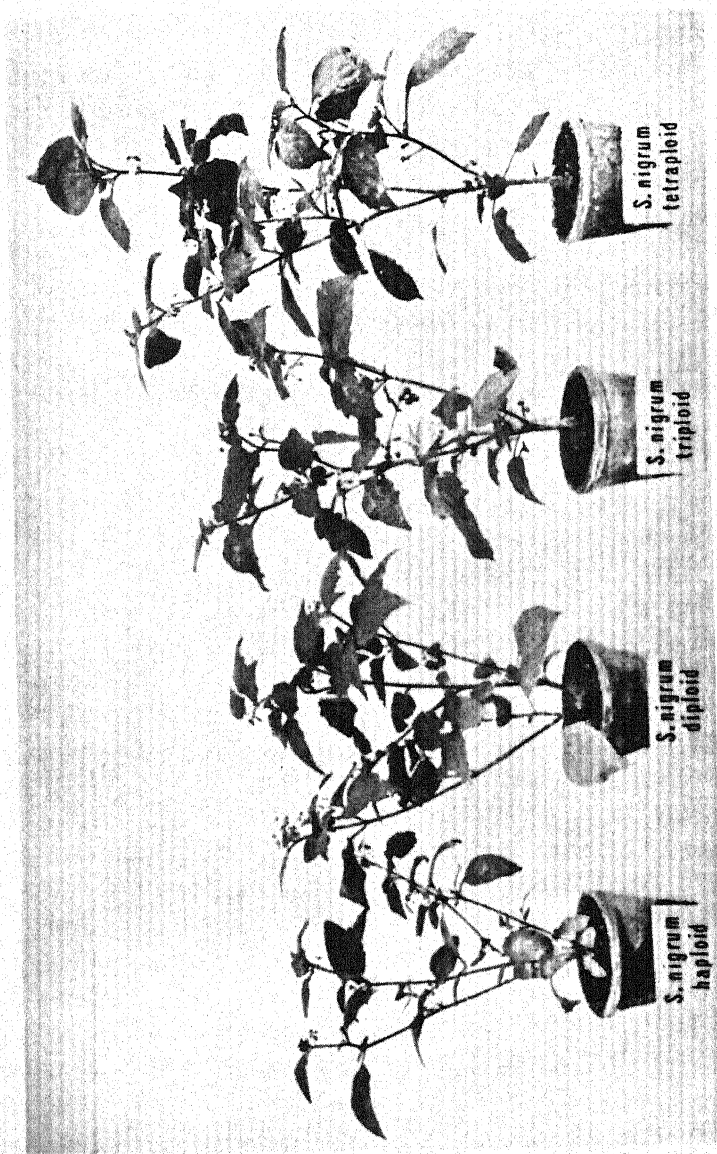


FIG. 11.—A POLYPLOID SERIES IN *SOLANUM NIGRUM* (BLACK NIGHTSHADE).

Plants with different chromosomes (x , $2x$, $3x$, and $4x$), showing the increase in size with increasing chromosome numbers. (After Jørgensen, 1928, *J. Genet.*, 19.)

was the name given to the plant on its second appearance.¹

The tetraploid *Primula sinensis* has appeared among seedlings of diploids three or four times during the past thirty years. The rarity with which it has been produced limits its variation. The large number of different colours found in the diploid cannot all be brought into the tetraploid because, unlike *Campanula persicifolia* and *Solanum* tetraploids, the giant *Primula* will cross with its diploid form only with the greatest difficulty. The tetraploid giant evening primrose has arisen frequently from the ordinary *Oenothera Lamarckiana* during the forty years that it has been under close observation by De Vries and others.

The tetraploid *Primula obconica* differs from all the other types mentioned in not being giant. It is not distinguishable by eye from its diploid relatives. The reason for this is probably that the strain from which it arose was heterozygous for dwarfing factors which have segregated and been selected in the tetraploid seedlings; for a dwarfing factor may counteract the giant-provoking influence of the four sets of chromosomes characteristic of the tetraploid.

It has been shown that in the chromosome sets of diploids there are chromosomes of different kinds, each of which is represented twice, one of the two being derived from the egg and the other from the pollen. The constitution of plants with different numbers of chromosomes may be shown symbolically if these different chromosomes are represented by the letters *A* to *G* in a plant such as *Oenothera*, *Matthiola*, *Rosa* or *Rubus*, with seven chromosomes in its "basic" haploid set, as follows :—

¹ *The Gardeners' Chronicle*, 1916, Vol. LX, p. 88.

Haploid (x).	Diploid ($2x$).	Trisomic ¹ ($2x + 1$).	Triploid ($3x$).	Tetraploid ($4x$).
A	AA	AAA or AA	AAA	AAAA
B	BB	BB BB	BBB	BBBB
C	CC	CC CC	CCC	CCCC
D	DD	DD DD	DDD	DDDD
E	EE	EE EE	EEE	EEEE
F	FF	FF FF	FFF	FFFF
G	GG	GG GG	GGG	GGGG

¹ Seven possible types, two given.

When the diploid plant forms its germ-cells, these pairs come together and only one of them passes into a particular germ-cell. Hence, in a hybrid where the corresponding chromosomes differ, if one is called A , and the other a , half the germ-cells have A , and half a , and from these germ-cells we get a new generation in the proportions $1AA$ to $2Aa$ to $1aa$, or three showing the dominant character to one showing the recessive. This is the simple Mendelian segregation and recombination already discussed.

But in the giant plants there are four sets of similar chromosomes. Each chromosome can pair with any one of the other three, and it may, as a matter of fact, associate with all three to form a single group—either a chain or a ring or cross. As a rule, two of these chromosomes go to one pole and two to the other. It follows that when a plant such as this is hybrid for one character $A-a$, germ-cells of several different kinds can be formed. Take the case where the four chromosomes of the one type are in the proportions $AAaa$. Germ-cells can be produced having the compositions AA , Aa , aa ; and these will be in the proportions 1-4-1 if, as we believe, the assortment is at random. Instead of half the germ-cells carrying the pure recessive character, only one-sixth will do so, and therefore only one in thirty-six of the progeny. This was first shown in *Primula sinensis* by Gregory (*l.c.*), and subsequently



in the thorn apple, *Datura Stramonium*, by Blakeslee and his collaborators (*l.c.*), and also in the tomato, *Solanum Lycopersicum* (Jørgensen, *l.c.*).

For example, in the tomato the form "potato leaf" is a simple Mendelian recessive occurring in a quarter of the second generation (F_2) progeny in diploids. But a tetraploid ($AAaa$) derived from doubling the chromosome complement of a heterozygous diploid (Aa) gave, not one in four, but actually two in fifty-three (Jørgensen, *l.c.*). This is evidently something like the expected one in thirty-six ratio. Other factors giving the same kind of inheritance are those for branched inflorescence and fruit-shape (Sansome, unpublished).

The same is probably true of all characters and all combinations in these simple tetraploid plants. Segregation depends on the random association of the four chromosomes which are concerned with each factor. The result of this is that when polyploid varieties are crossed, very much larger families are necessary in the second generation if any of the recessive characters are to be recovered.

In general, the type $AAaa$ resembles the diploid type Aa , but the new proportions found in the combination $Aaaa$ often show that although dominance may be complete in the diploid, it need not be so in the tetraploid. For example, in the case of the factor for inhibiting petal sap colour in *Primula sinensis*, this combination gives a pink colour in the normal type, *i.e.*, is intermediate between the dominant (white) and recessive (red), (de Winton and Haldane, 1930¹).

It has been mentioned that the chromosomes often come together in fours at reduction in these tetraploids. In *Primula sinensis* (Darlington, 1930²), and in *Datura*

¹ *J. Genet.*, 22.

² *Ibid.*, 23.

(Belling, 1927¹), it is common to find the forty-eight chromosomes of the tetraploid united in twelve groups

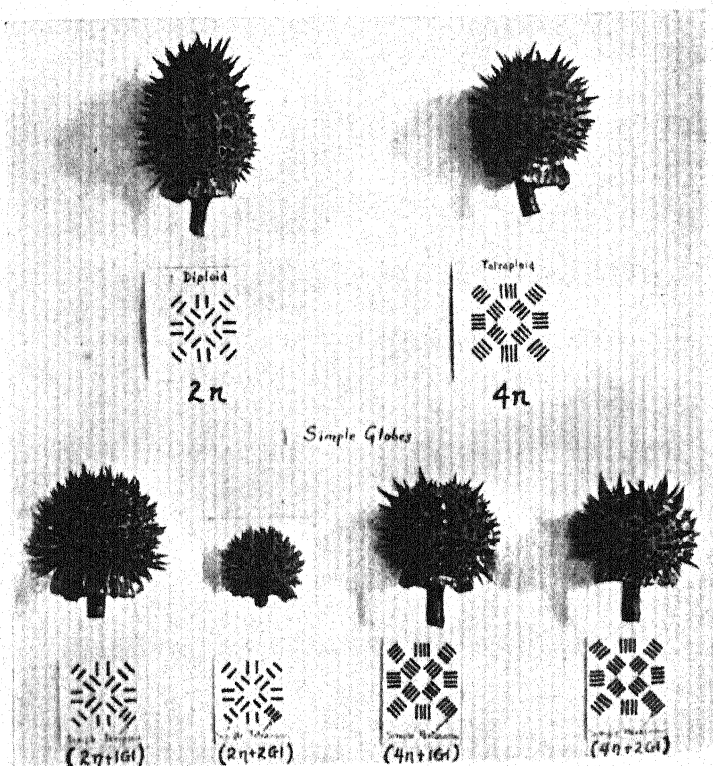


FIG. 12.—FRUITS OF *DATURA* TYPES.

Fruits of diploid and tetraploid *Datura Stramonium* and of seedlings from them having one and two extra chromosomes of a particular type ("G") producing what is called the "globe" mutant with flatter fruit. The tetraploid fruit is smaller than the diploid, and the extra-chromosome forms of diploid and tetraploid are smaller than the corresponding normals. The chromosome complement of each plant is shown beneath its fruit. For $2n$ and $4n$, read " $2x$ " and " $4x$." (From Blakeslee, 1922, *Amer. Nat.*, 56, 16-31.)

of four. These groups usually divide into two and two. But occasionally they divide into three and one.

¹ *J. Genet.*, 18.

The result of this is the formation of germ-cells with odd numbers of chromosomes. And, as has been pointed out already, germ-cells with odd numbers, just like the plants themselves, are unbalanced. They do not grow so well. Consequently, where germ-cells are formed with irregularities of this kind, a reduction of fertility is to be expected. This is what we do find, and, together with it, the appearance of occasional odd-

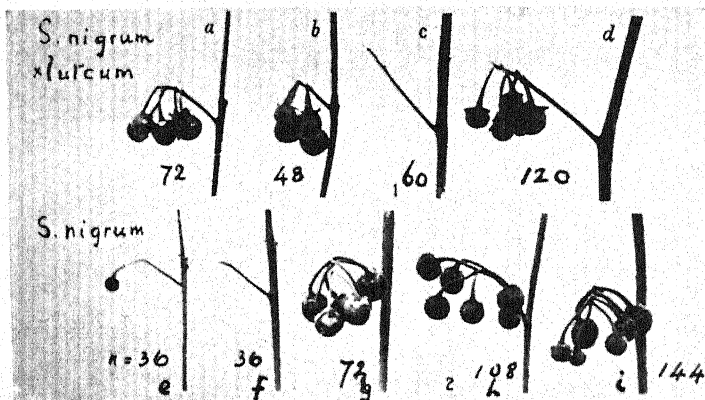


FIG. 13.—HYBRID AND NON-HYBRID *SOLANUM* FRUITS.

Fruits from hybrid and non-hybrid forms of *Solanum* with different chromosome numbers. *a*, "diploid" *S. nigrum*; *b*, *S. luteum*; *c*, their "diploid" hybrid; *d*, their tetraploid hybrid; *e* and *f*, haploid *S. nigrum*; *g*, diploid; *h*, triploid; *i*, tetraploid. The fruits of the non-hybrid tetraploid are smaller than those of the diploids. The chromosome number of each plant is given under its fruit. The fact that the diploid *S. nigrum* is hexaploid ($6x$) and the diploid *S. luteum* is tetraploid ($4x$) in remote origin from ancestors with 24 chromosomes can be neglected for present purposes because they each behave like true diploids (*v. Chap. XI*). (After Jørgensen, 1928, *J. Genet.*, 19.)

chromosome types which are distinguishable by their leaf and fruit characters in the tetraploid *Datura* as in the diploid. All the tetraploids referred to above are therefore definitely less fertile than the diploids from which they arose (Figs. 12 and 13). In consequence, although they are giants in every other respect, their

fruits, where they depend on seed production, are under-developed. This means that the tetraploid tomato is relatively unprofitable in cultivation, although the giant *Primula sinensis* and the *Campanula* Telham Beauty, with their larger flowers, are, of course, important horticultural improvements; albeit that their seeds being produced less abundantly, these tetraploid varieties are more expensive.

secreting meal; the corolla is pale yellow and shining; the flowers scented; the leaves smooth and acutely toothed. *Primula floribunda*, a native of Afghanistan, is half the height of the other species; the glands secrete no meal; the petals are deeper yellow, and the flower is scentless; the leaves are rough, very hairy, and

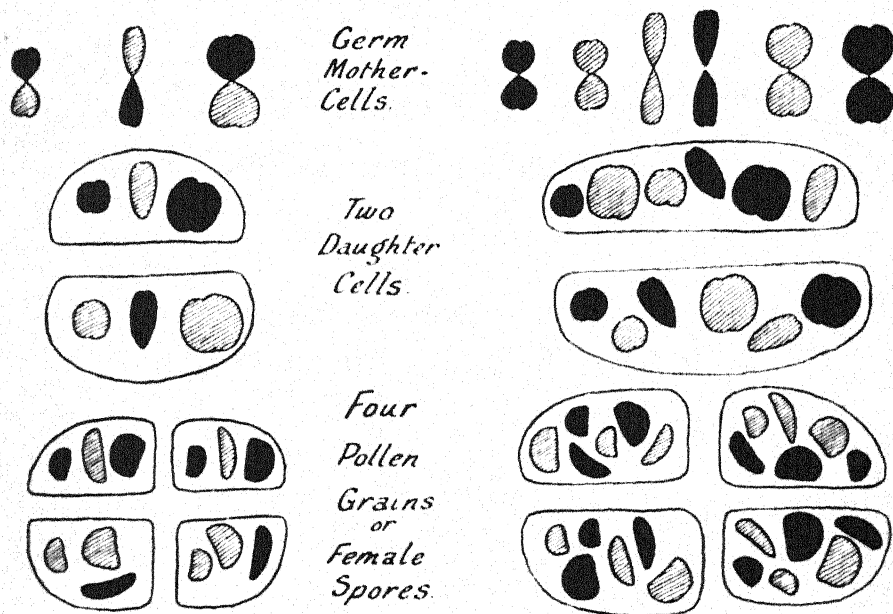


FIG. 14.—PAIRING IN DIPLOID AND TETRAPLOID HYBRIDS.

Diagram of segregation in diploid and tetraploid hybrids (type: *Primula kewensis*). In the diploid (left), dissimilar chromosomes pair and pass to opposite germ-cells to give various unsatisfactory new combinations. In the tetraploid (right), similar chromosomes pair, so that all the germ-cells are alike, and the plant therefore fertile and true-breeding. (From Buxton and Darlington, 1932, *New Phyt.*)

crenately toothed. The hybrid is about the same size as the larger parent, but in general character it is intermediate. In both species and in the hybrid nine pairs of chromosomes are found at reduction. In the hybrid,

germ-cell formation is regular, but the result is complete sterility. Corresponding chromosomes of *P. verticillata* and *P. floribunda* pair and pass to opposite poles, so that every germ-cell has nine chromosomes. But some of these will be from one species and some from the other. Evidently the fact has to be reckoned with that the chromosomes of different species never do exactly correspond. Chromosome No. 1 of *P. verticillata* may lack *something* necessary for the plant's development which is present in chromosome No. 2. But, when it finds itself together with chromosome No. 2 of *P. floribunda*, that *something* may still be lacking.

In a hybrid between two *Crepis* species, Navashin (1927¹), was able to show from examining the chromosomes that this was the case—the only seedlings raised were those from germ-cells with chromosomes of one species—unadulterated by those of the other. The *Primula* hybrid is absolutely sterile with pollen of both parent species, but *P. floribunda* has set occasional seeds with pollen of the hybrid, giving offspring very like itself. As in the *Crepis* hybrid, occasional germ-cells are formed containing the unadulterated set of one of the parents, but naturally these are very rare (see Fig. 14, left-hand column).

Three times the hybrid has set seeds on selfing, and each time in abundance. But all the seedlings raised were different from the parent. They were all giant (about twice the size of the diploid parent), highly fertile (a single capsule produced as many as 170 seeds) and almost true-breeding. The gigantism at once suggests tetraploidy by analogy with the giant *Primula sinensis*. In the last case the branch that had sported to fertility was examined and found to be tetraploid; thirty-six

¹ Zeits. Zellforsch. mik. Anat., 4.

chromosomes were found at mitosis. The seedlings also proved to be tetraploid. Clearly the same kind of change had taken place in the branch of the *Primula* as was found in the callus of the tomato. The chromosome number had doubled at a mitosis in the growing-point (cf. Fig. 15).

Gigantism is a normal and perhaps universal property

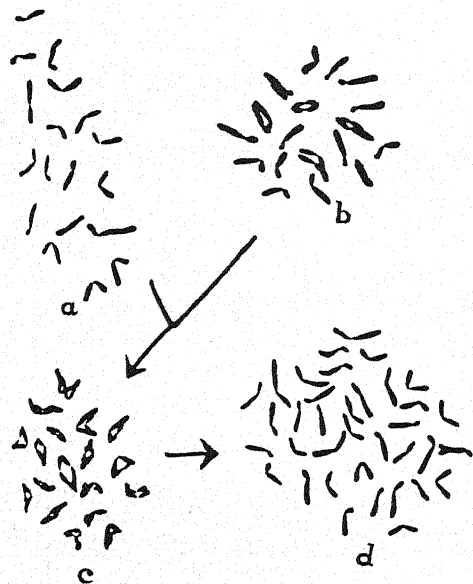


FIG. 15.—CHROMOSOMES OF *PRIMULA KEWENSIS*.

Diploid (c); tetraploid (d); and its two parents, *P. floribunda* (a) and *P. verticillata* (b). The chromosomes are just dividing (anaphase) in (b) and (c). (After Newton and Pellew, 1929, *J. Genet.*, 20.)

of those tetraploids which can be compared directly with the diploids from which they have arisen. But its association with fertility and true-breeding in a hybrid is something new. If our theory of the sterility of the diploid is correct, the tetraploid must be fertile because like chromosomes regularly pair with like: *floribunda* with *floribunda*, and *verticillata* with *verticillata*. When

reduction is studied in the tetraploid hybrid, it is found that instead of coming together in fours, as in the *Primula sinensis* tetraploid, the chromosomes associate in pairs for the most part. Clearly the chromosomes of the two species can pair in the absence of competition, but when after doubling each has an identical mate, the chromosomes of the species leave one another alone (see Fig. 14, right-hand column). Like pairs with like (f with f and v with v) and there is no segregation, no sterility. The giant hybrid is $ffvv$, and every one of its germ-cells is fv in respect of each of the nine chromosome types. Its general behaviour is therefore that of a diploid species with the "haploid" chromosome number of 18. Occasionally one or two rings of four are formed, where all four chromosomes of one type come together ($ffvv$). In these cases two chromosomes of the same species may pass to one pole, leaving their mates of the other species to pass to the other pole; there will be segregation of the characters of the species if the germ-cells that are produced in this way live and play their part in seed formation. Also if the ring does not divide equally, we shall expect to find seedlings with odd numbers of chromosomes as in the simple tetraploids. Such seedlings have been found.

These are broadly the two types of segregation that are found in *Primula kewensis*. Of the original seedlings from the fertile branch not more than ten per cent. showed any very marked variation. Half of these probably had one chromosome too few or too many and had peculiarities of leaf-shape and habit, unlike either of the parental species. They differed from the normal tetraploid hybrid in the same way as the extra-chromosome tomatoes differ from the normal. The other half had the normal number of chromosomes, but

varied in regard to mealiness or some other difference distinguishing the two species. These were evidently the result of *P. verticillata* chromosomes pairing with *P. floribunda* and giving a segregation of the characters distinguishing the two species.

It follows from the foregoing that sterility, or more properly *generational* sterility (not due to malformed anthers or incompatibility of the pollen), is merely a symptom of segregation at the time the germ-cells are formed. If a hybrid can abolish segregation by doubling

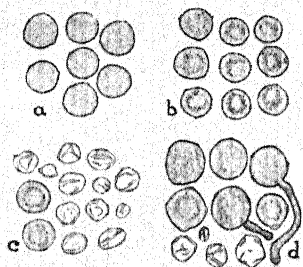


FIG. 16.—POLLEN-GRAINS OF *SOLANUM* SPECIES AND HYBRIDS.

Pollen-grains of *Solanum nigrum* (a), *S. luteum* (b), their diploid hybrid (c), and their tetraploid hybrid (d). Doubling of the chromosomes restores fertility to a sterile hybrid. (After Jorgensen, 1928, *J. Genet.*, 20.)

its chromosome number, it automatically abolishes sterility.

Thus it follows that, while doubling in a pure species reduces fertility by encouraging irregularities in segregation, doubling in a hybrid restores fertility simply by abolishing segregation, so far as it can abolish it (Figs. 14, 16 and 19). At the same time, the new tetraploid enjoys the advantages of a new combination of characters, a capacity to vary them by occasional segregation, a giant habit and hybrid vigour.

The new (tetraploid) form of *Primula kewensis* is

sharply distinguished both from the diploid hybrid and the parental species, and it has indeed every claim to be considered as a new species—the claim being especially good in this case because (as in *Primula sinensis*) the tetraploid will only cross with difficulty with one of the diploid forms (*P. floribunda*), and the result is a triploid ($3x$) of reduced fertility which gives back offspring with various abnormal numbers and unbalanced combinations of chromosomes. It owes its character as a species to the fact that it is a hybrid, for if it were not a hybrid it would be no innovation and, as we have seen, it would be less fertile than its parents and would be eliminated in nature.

It is evident that this kind of polyploid is likely to be of more importance than the non-hybrid kind where the plants are reproduced from seeds, on account of its greater fertility. It is therefore worth while looking at other cases of a similar kind that have occurred in the course of breeding experiments. Below is given a table of the seventeen best-authenticated examples. Some of the species used, it will be noticed, are already tetraploid relative to the species with which they are crossed, but this does not seriously affect the result, for these tetraploids usually behave even more like diploids than the tetraploid *Primula kewensis*.

In many of these cases it is possible to suppose that doubling took place at a division in the growing point of the young plant, as in *Primula kewensis*. But in (2), (7), (8), (13) and (17) this cannot be so, for the new giant fertile hybrid has a chromosome number which, although greater than the sum of the numbers found in the parental germ-cells, is not twice that number. A glance will show that in each of these cases it is equal to the sum of the haploid number of one parent and the diploid number

of the other. Evidently the germ-cell contributed by one parent must have had an unreduced number of chromosomes. How can this come about?

There are many ways in which germ-cells may be

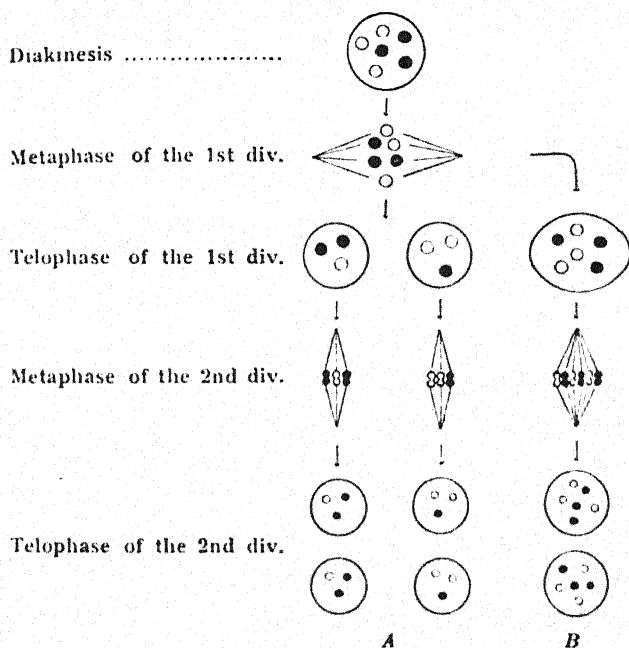


FIG. 17.—REDUCTION IN GERM-CELL FORMATION IN THE RADISH-CABBAGE HYBRID AND OTHER STERILE DIPLOIDS.

A, The usual course of division, giving sterile germ-cells; B, the formation of fertile diploid germ-cells by failure of reduction. (After Karpechenko, 1927, *Hereditas*, 8.)

formed without any reduction, and these have been demonstrated most clearly by Rosenberg (1926)¹ in the hawkweeds (*Hieracium* species) and by Karpechenko (1927)² in the radish-cabbage hybrid (No. 5 in table). These workers have found that chromosomes which have failed to pair in hybrids may lag behind on the

¹ *Hereditas*, 8.

² *Ibid.*, 9.

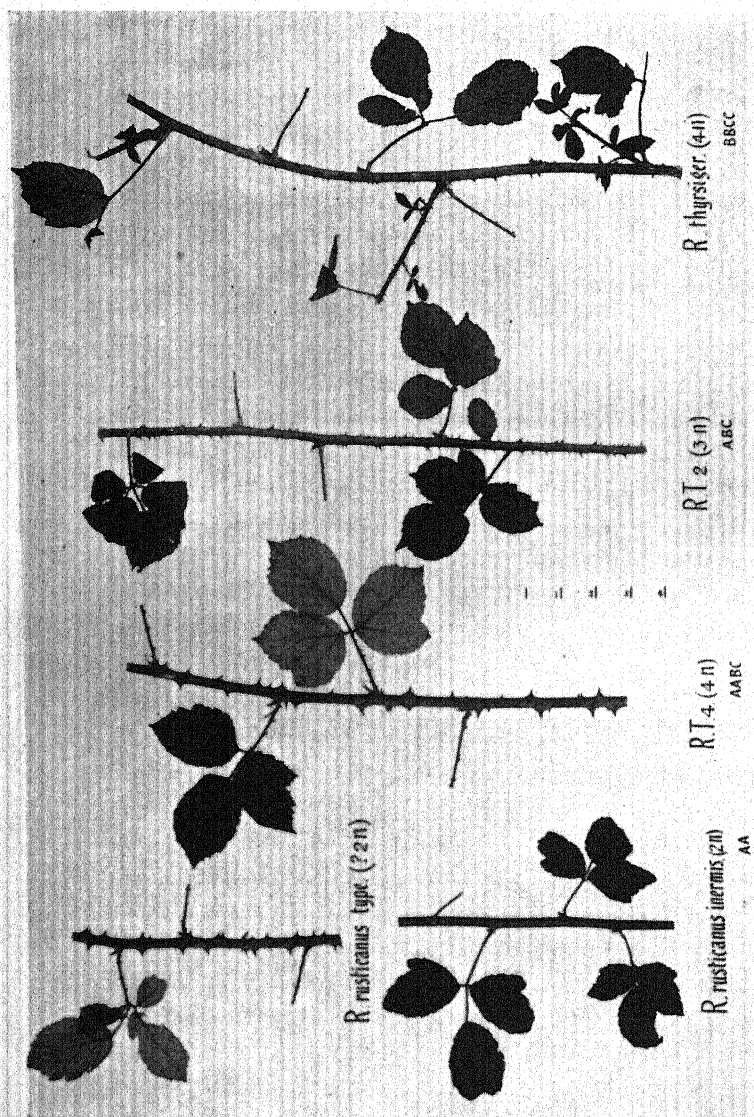
Hybrid (female parent first).	Chromosome Nos. at Mitosis.		Author.
	Before Doubling.	After Doubling.	
1. <i>Primula floribunda</i> ($\times = 9$) \times <i>P. verticillata</i> ($\times = 9$).	18 (F_1)	36 (F_2)	Newton and Pellew, 1929 (<i>J. Genet.</i> , 20 , 405-66). Goodspeed and Clausen, 1925 (<i>Genetics</i> , 10). Ichijima, 1926 (<i>Genetics</i> , 11 , 590-604). Tschermak and Bleier, 1926 (<i>Ber. deutsch. Bot. Ges.</i> , 44). Karpechenko, 1927 (<i>Bull. Appl. Bot.</i> , 17 (3), 305-408). Rybin, 1927 (<i>Bull. Appl. Bot.</i> , 17 , 191-240). Bremer, 1928 (<i>Arch. Suikerindustrie in Ned. Ind.</i>). Crane and Darlington, 1927 (<i>Genetica</i> , 9 , 241-77).
2. <i>Nicotiana glutinosa</i> ($\times = 12$) \times <i>N. Tabacum</i> ($\times = 24$).	36 (F_1)	72 (F_2)	
3. <i>Fragaria bracteata</i> ($\times = 7$) \times <i>F. Hecleri</i> ($\times = 7$).	14 (F_1)	28 (F_2)	
4. <i>Agriopsis ovata</i> ($\times = 14$) \times <i>Triticum durum</i> ($\times = 14$) and \times <i>T. dicoccoides</i> ($\times = 14$).	28 (F_1)	56 (F_2)	
5. <i>Raphanus sativus</i> ($\times = 9$) \times <i>Brassica oleracea</i> ($\times = 9$).	18 (F_1)	27, 36 (F_2)	
6. [<i>Nicotiana Tabacum</i> ($\times = 24$) \times <i>N. rustica</i> ($\times = 24$).] \times <i>N. rustica</i> ($\times = 24$).	—	72 (F_1)	Buxton and Newton, 1928 (<i>J. Genet.</i> , 19 , 269-79). Jorgensen, 1928 (<i>J. Genet.</i> , 19 , 133-211). Marsden-Jones and Turrill, 1928 (<i>Nature</i> , 122). Whyte, 1930 (<i>J. Genet.</i> , 23). Levitsky and Benczeaka, 1929 (<i>Proc. U.S.S.R. Cong. Genet. Leningrad</i> , 2 , 345-52). Rybin, 1929 (<i>Ber. Deutsch. Bot. Ges.</i> , 17). Emerson and Beadle, 1929 (<i>Amer. Nat.</i> , 63 , 289-300). Tschermak, 1930 (<i>Ber. deutsch. Bot. Ges.</i> , 48). Gregor and Sansome, 1930 (<i>J. Genet.</i> , 22 , 373-86). Müntzing, 1930 (<i>Hereditas</i> , 14 , 153-72). Frandsen and Winge, 1932 (<i>Hereditas</i> , 16).
7. <i>Saccharum officinarum</i> ($\times = 40$) \times <i>S. spontaneum</i> ($\times = 56$).	—	96 (F_2) ¹	
8. (a) <i>Rubus rusticus inermis</i> ($\times = 7$) \times <i>R. thyrsiger</i> ($\times = 14$).	—	28 (F_1)	
(b) <i>Rubus rusticus</i> ($\times = 7$) \times <i>R. Idaeus</i> ($\times = 7$).	—	28 (F_1)	
9. <i>Digitalis purpurea</i> ($\times = 28$) \times <i>D. ambigua</i> ($\times = 28$).	56 (F_1)	112 (F_2)	
10. <i>Solanum nigrum</i> ($\times = 36$) \times <i>S. latum</i> ($\times = 24$).	60 (F_1)	120 (F_2)	Cong. Genet. Leningrad, 2 , 345-52). Rybin, 1929 (<i>Ber. Deutsch. Bot. Ges.</i> , 17). Emerson and Beadle, 1929 (<i>Amer. Nat.</i> , 63 , 289-300). Tschermak, 1930 (<i>Ber. deutsch. Bot. Ges.</i> , 48). Gregor and Sansome, 1930 (<i>J. Genet.</i> , 22 , 373-86). Müntzing, 1930 (<i>Hereditas</i> , 14 , 153-72). Frandsen and Winge, 1932 (<i>Hereditas</i> , 16).
11. <i>Saxifraga rosacea</i> ($\times = 16$) \times <i>S. granulata</i> ($\times = 16$).	32 (F_1)	64 (F_2)	
12. <i>Triticum vulgare</i> ($\times = 21$) \times <i>Secale cereale</i> ($\times = 7$).	28 (F_1)	56 (F_2)	
13. <i>Nicotiana Tabacum</i> ($\times = 24$) \times <i>N. glauca</i> ($\times = 12$).	36 (F_1)	72 (F_2)	
14. <i>Eschscholera perennis</i> ($\times = 20$) \times <i>Zea Mays</i> ($\times = 10$).	—	40 (F_2)	
15. <i>Triticum turgidum</i> ($\times = 14$) \times <i>T. villasum</i> ($\times = 14$).	21 (F_1)	42 (F_2)	Cong. Genet. Leningrad, 2 , 345-52). Rybin, 1929 (<i>Ber. Deutsch. Bot. Ges.</i> , 17). Emerson and Beadle, 1929 (<i>Amer. Nat.</i> , 63 , 289-300). Tschermak, 1930 (<i>Ber. deutsch. Bot. Ges.</i> , 48). Gregor and Sansome, 1930 (<i>J. Genet.</i> , 22 , 373-86). Müntzing, 1930 (<i>Hereditas</i> , 14 , 153-72). Frandsen and Winge, 1932 (<i>Hereditas</i> , 16).
16. <i>Phleum pratense</i> ($\times = 7$) \times <i>P. alpinum</i> ($\times = 14$).	21 (F_1)	42 (F_2)	
17. [<i>Galeopsis pubescens</i> ($\times = 8$) \times <i>G. speciosa</i> ($\times = 8$)] \times <i>G. pubescens</i> ($2x = 24$).	—	24 (F_2)	
18. <i>Brassica Napus</i> ($\times = 18$) \times <i>B. campestris</i> ($\times = 10$).	—	32 (F_2)	
	28 (F_1)	56 (F_2)	

¹ Derivatives of this plant are now the principal source of sugar production in Java.

plate after the paired chromosomes have passed to the two poles. They then form, as it were, a bridge between the two daughter nuclei, which therefore run together and form a single nucleus. All the chromosomes then divide once at the second division, which is just like mitosis in a vegetative cell. For most genetic purposes it is as though there had been no reduction division at all, and the germ-cells (only two are formed from each mother-cell in this case) have the unreduced diploid chromosome number (Fig. 17).

Such germ-cells are clearly responsible for the tetraploids in the four instances mentioned, because we can see precisely the preponderant influence of one of the parents that we should expect. For example, in the *Rubus* cross three seedlings were raised. Two of these had the expected twenty-one chromosomes, *i.e.*, the sum of the numbers in the germ-cells of the two parents. The third had twenty-eight; it was tetraploid, and it is to be supposed that its female parent contributed a germ-cell to its formation with fourteen instead of seven chromosomes. The tetraploid had four characters derived from its mother that were not shown by either of its sister-seedlings (Fig. 18), *viz.*, (1) a restricted distribution of prickles; (2) the absence of stalked glands on the stems; (3) the absence of small prickles, "acicles"; and (4) the felted hairs on the under-surface of the leaf. Obviously the influence of a species in crossing is proportionate to the number of chromosome sets it contributes—a conclusion which tallies very well with what has been seen already in the case of haploids.

Example No. 6 is more complicated. First the *Nicotiana Tabacum* contributed an unreduced egg-cell when crossed with *N. rustica*; the hybrid therefore resembled its female parent more closely and had

FIG. 18.—*RUBUS* HYBRIDS.

Branches of the tetraploid and triploid hybrids between two *Rubus* species, showing their influence proportionate to the chromosome sets contributed. *A*, set of *Rubus rusticanus* ($2x$); *BC*, set of *Rubus thyriger* ($4x$). *R. rusticanus* var. *inermis*, without prickles (a recessive character), was used as a parent, but carried factors giving a restricted distribution of prickles on its seedling, *R.T.4* ($4x$), but not on *R.T.2* ($3x$). For "*n*" read "*x*." (After Crane and Darlington, 1927, *Genetica*, 9.)

seventy-two chromosomes. Then the hybrid contributed another unreduced egg-cell when back-crossed with *N. rustica*. The second generation was therefore intermediate between the two species. In this way the same result as that found in *Primula kewensis* was reached in two steps.

There can be little doubt that in *Digitalis*, *Triticum*, *Phleum* and *Raphanus-Brassica* also the tetraploid owed its origin to the production of unreduced germ-cells, but in these hybrids the failure of reduction occurred on both male and female sides in the first generation (F_1). But whichever way the unreduced germ-cells arise, if the chromosomes of each type have a similar mate to pair with, the result is fertility and true breeding. In fact, the tetraploid *Rubus* has better pollen, is more fertile and has, consequently, much larger fruits than either of its parents.

In the *Saxifraga* hybrid, No. 11 (Marsden-Jones and Turrill, 1930¹), it was a question of crossing species of different sections of the genus with a range of distribution overlapping in the mountains of Western Europe. *S. rosacea* is an evergreen species reproducing by green offsets, while *S. granulata*, a plant native in England, with a double form that is commonly cultivated, has a resting period in the summer during which it is carried on by bulbils or gemmae. *S. granulata* is the larger species in leaf, flowering-stem and flower. The F_1 generation of twenty-six plants was uniform, and intermediate between the parents. Only one of the plants set seeds, and on selfing it gave rise to over four hundred seedlings; these were of stouter growth than the parent and again uniform, except in minor points, *i.e.* they showed no tendency to revert to the characters of the two parental

¹ *J. Genet.*, 23, 83-92.

species. These seedlings proved to have double the chromosome number of their parent (Whyte, 1930¹). This case is strictly analogous to that of *Primula kewensis*. The uniformity seems to justify the new tetraploid being considered a new species, and it has been called *Saxifraga potternensis*.

Perhaps *Raphanus-Brassica* is the most striking of all cases of true-breeding fertile hybrids. It is easy enough to obtain seedlings by using the pollen of the cabbage on the common radish, but these seedlings are usually sterile. Karpechenko obtained one hundred and twenty-three hybrid seedlings from two hundred and two cross-pollinations, and they set no seeds the first year. Transplanted, they set natural seeds in the latter part of the following year. One plant gave as many as one hundred and eighty-nine seeds, but fertility was never high; rather it was sporadic. These seedlings proved to be either tetraploid (with thirty-six chromosomes) when they resembled first generation plants except in being sturdier and bigger, or triploid, when they showed a decided leaning towards the radish side. The latter were back-crosses with the radish parents growing in the neighbourhood. There can be no doubt that these seedlings were due to what we may call the *accidental* formation of germ-cells with unreduced chromosome numbers, the whole course of which was worked out by Karpechenko. If we represent a set of radish chromosomes as R , and a set of cabbage as B , the F_1 was RB , and the F_2 tetraploid $RRBB$ and the triploid RRB .

The most remarkable of the differences between the two genera *Raphanus* and *Brassica* is in the fruit, and is one of great significance to systematists. In both the pod may be regarded as of two parts, a dehiscent, two-

¹ *J. Genet.*, 23.

chambered lower part and an indehiscent, single-chambered upper part. In the radish the upper part is developed to the exclusion of the lower part, which is

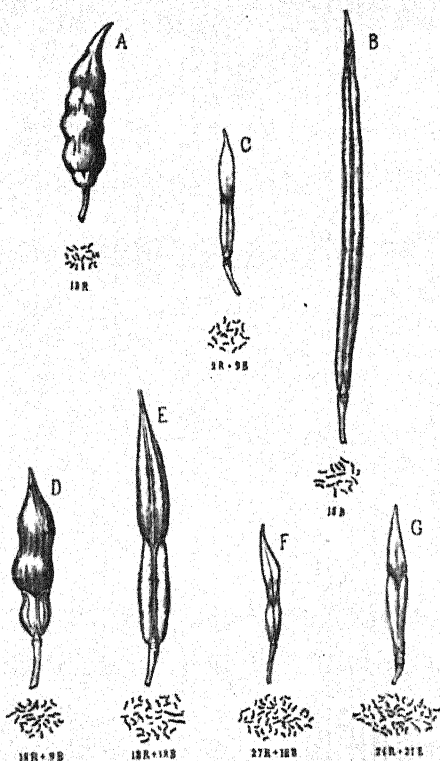
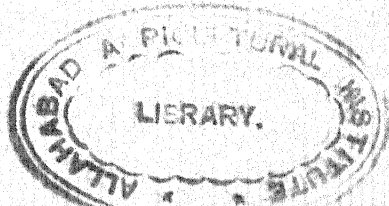


FIG. 19.—FRUITS OF RADISH AND CABBAGE AND THEIR HYBRIDS, WITH THE CHROMOSOME SETS OF EACH.

R is a radish and B a cabbage chromosome set. The influence of the two parents on the shape of the fruit is proportionate to the number of chromosomes contributed. C is the F_1 with nine chromosomes from each parent; E is the F_2 with 18 chromosomes from each; D is the back-cross to the radish with two radish sets and one cabbage; F is a derivative with three radish and two cabbage sets; G is an unbalanced form. (From Karpechenko, 1927, *Bull. App. Bot.*, Leningrad, 17, 3.)

sterile, and in the cabbage the lower part is developed and the upper part sterile or nearly so. The tetraploid



RRBB was intermediate; half the fruit was two-valved cabbage and the other half was valveless radish. The triploid RRB was two-thirds radish fruit, and one-third cabbage (Fig. 19). This shows how the build of a plant depends just on which chromosomes have been contributed to it at fertilisation.

Another *Brassica* tetraploid is likely to be of great agricultural interest, that produced by crossing the turnip and the swede. It is like the rest, giant and intermediate.

It may be thought that, in spite of the constant agreement between theory and observation, it is not the doubling of the chromosomes that leads to the restoration of fertility, but that the relationship is quite accidental, or the other way round. It might be suggested, for example, that something outside the chromosomes restores the fertility, and doubling their number is a consequence.

A recent observation offers a critical test of the alternative explanations. Hybrids, usually sterile, have often been obtained between species of *Digitalis*. One case, described in detail by Neilson Jones (1912),¹ shows that marked differences occur between seedlings obtained by crossing the species in opposite ways. Buxton and Newton (1928)² raised numerous seedlings of the same hybrid between *Digitalis purpurea*, the ordinary foxglove, and *D. ambigua*, a yellow-flowered species from Southern Europe (Fig. 20). They were intermediate in character and almost entirely sterile. They had the same chromosome number as their parents, fifty-six. The few seeds that two of them set on selfing gave seedlings that were highly fertile and bred true. They were uniform in character and of giant size. As in other tetraploids, it was found that the proportions of the

¹ *J. Genet.*, 3.

² *Ibid.*, 18.

giant were slightly different from those of its parent. It was more robust. This difference is in exactly the opposite direction to that found between the haploid stocks and tomatoes and their normal diploid relatives.

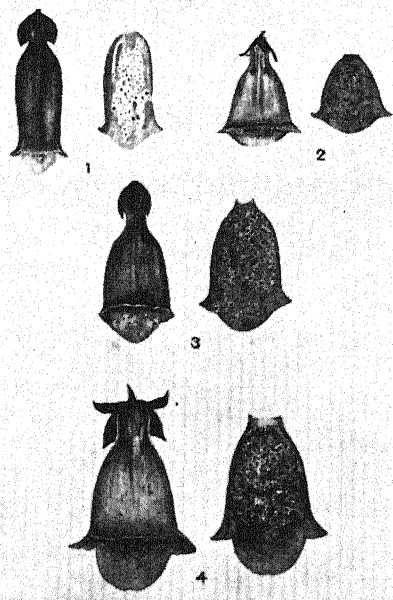


FIG. 20.—DIPLOID AND TETRAPLOID FOXGLOVES.

1, *Digitalis purpurea* (foxglove); 2, *D. ambigua*; 3, a diploid F_1 hybrid; 4, the giant tetraploid F_2 hybrid. (From Buxton and Newton, 1928, *J. Genet.*, 19.)

The general size, however, is exactly doubled. For example, the corolla of the flower is a quarter again as broad, a quarter again as long, and we may presume a quarter again as thick. It is therefore twice the bulk. These seedlings were tetraploid, having one hundred and twelve chromosomes. Evidently the first generation had been entirely sterile in the ordinary sense; the only

germ-cells that had played their part were those that had undergone no reduction and therefore, of course, no segregation. In such circumstances almost any hybrid may be fertile. The fertile tetraploids were back-crossed with the pollen of the parent species and a number of triploid seedlings raised. But among these was one diploid. It resembled the sterile diploid of the first generation in leaf and flower, and was itself completely sterile. There can be no doubt that the pollen of the parent had stimulated the development of a reduced (diploid) egg-cell of the tetraploid by parthenogenesis, as in the other cases described earlier. The first generation had missed reduction and gained fertility, the second had missed fertilisation and lost its fertility again (Buxton and Darlington, 1931¹). In view of these observations it is impossible to doubt that the accidents that affect chromosome number affect form and fertility as a *result* of this.

Most of these hybrid polyploids breed very much as *Primula kewensis* does. In some characters the intermediate form is preserved, the parental types never reappear, and this is particularly the case in the radish-cabbage hybrid where no rings of four chromosomes are formed. In other hybrid polyploids segregation of the kind found in *Primula sinensis* or the tomato occurs in some of the characters distinguishing the parents; the recessive appears once in thirty-six times. The constitution of the *Rubus* hybrid was *AAaa* in regard to the "armed" or prickled character. Two chromosomes from *R. thyrsiger* carried the factor *A* for prickles and two from *R. rusticanus* carried the factor *a* for no prickles. Out of four hundred and ninety seedlings, nineteen were completely devoid of prickles. If this factor had been

¹ *Nature*, 127.

in a chromosome of one species which would not pair with its opposite number of the other species, there would never have been any unprickled seedlings, no matter how many had been raised. This was actually the case with the character "stalked glands" of *R. thyrsiger*, which never reappeared in any of the descendants (Fig. 18).¹

These examples, largely from investigations in the past five years, show the kind of result a breeder has to look out for when he is crossing species which usually give sterile hybrids. A cross between two diploid species (except in certain genera), or between a diploid and tetraploid, is nearly always infertile. When he crosses species he should therefore know whether they are diploid or polyploid to begin with. If he raises a sterile hybrid which is of no use to him because he cannot propagate it vegetatively, let him look out for the odd seed which will give him his new race, a giant and fertile polyploid.

¹ Crane and Darlington, 1932, *Nature*, 129.

CHAPTER XII

POLYPLOID SPECIES

THE great vigour and fertility of tetraploid hybrids naturally set us wondering what part such tetraploids may have played in the origin of cultivated plants. The chromosome numbers of many thousands of species and varieties of cultivated plants have been ascertained, and it may be stated at once that the majority of them have chromosome numbers that are polyploid, that is to say, they are higher multiples than two of the lowest or "basic" haploid chromosome number found among their relatives. They are called triploid, tetraploid, pentaploid, hexaploid, heptaploid and octoploid, according as the numbers are 3, 4, 5, 6, 7 or 8 times the basic number, or they may be stated, for short, to be $3x$, $4x$, $5x$, $6x$, $7x$, $8x$ and so on.

A few important new examples are given in the accompanying table; for authorities reference should

x .	Diploid Forms.	Polyploid Forms.
10	<i>Vallisneria spiralis</i>	<i>V. gigantea</i> ($4x$).
10	<i>Zea Mays</i> (Indian corn)	<i>Euchlaena perennis</i> ($4x$).
9	<i>Canna indica</i>	<i>Canna</i> vars. ($3x$).
	<i>Pbleum pratense</i> (Britain, dwarf tim-	<i>P. pratense</i> ($6x$) (U.S.A., tall).
7	othy grass)	
	<i>P. alpinum</i> (Sweden)	<i>P. alpinum</i> ($4x$) (Britain).
	<i>Avena barbata</i>	<i>A. abyssinica</i> ($4x$).
7	<i>A. brevis</i>	<i>A. sativa</i> ($6x$) (cultivated oat).
	<i>A. strigosa</i>	<i>A. fatua</i> ($6x$) (wild oat).
7	<i>Festuca elatior</i> (meadow fescue)	<i>F. elatior</i> vars. ($4x$, $6x$, $10x$).
7	<i>Triticum monococcum</i> (small spelt wheat).	<i>T. dicoccum</i> ($4x$) (emmer wheat).
		<i>T. turgidum</i> ($4x$) (rivet wheat).
		<i>T. durum</i> ($4x$) (macaroni wheat).
		<i>T. vulgare</i> ($6x$) (bread wheat).
		<i>T. Spelta</i> ($6x$) (spelt wheat).
6	<i>Tradescantia crassifolia</i>	<i>T. virginiana</i> ($4x$) (spiderwort).

x.	Diploid Forms.	Polyploid Forms.
12	<i>Tulipa australis</i> <i>T. Hageri</i> <i>T. Gesneriana</i> <i>T. Clusiana</i> (Thibet) Garden vars.	<i>T. sylvestris</i> (4x). <i>T. Wittallii</i> (4x). Garden vars. (3x). <i>T. Clusiana</i> (4x and 5x) (Europe). <i>T. praecox</i> (3x). <i>T. saxatilis</i> (3x).
	<i>Hyacinthus orientalis</i> , Hort.	<i>H. orientalis</i> , Hort. (3x, ca. 4x, etc.)
	<i>Narcissus Tazetta</i>	<i>N. Tazetta</i> (ca. 3x).
	<i>Iris variegata</i> <i>I. pallida</i>	<i>I. florentina</i> (3x). <i>Iris</i> , cultivated vars. (4x + 5x +, etc.).
12	<i>I. Kaempferi</i>	
	<i>Musa sapientum</i>	<i>Musa paradisiaca</i> vars. (3x, 4x, 5x) (banana). <i>C. sativa</i> vars. (4x).
10	<i>Cannabis sativa</i> (hemp)	<i>P. nudicaule</i> var. <i>striatocarpum</i> (10x).
7	<i>Papaver Rhoeas</i> (cornfield poppy)	<i>P. dubium</i> (4x).
	<i>P. nudicaule</i> (Iceland poppy) Shirley poppies	
9	<i>Brassica oleracea</i> (cabbage, etc.)	<i>B. Napus</i> (4x) (rape).
10	<i>Brassica Rapa</i> (swedes and turnips)	
16	<i>Nasturtium officinale</i>	Edible watercress (3x) (and 4x).
8	<i>Prunus avium</i> (sweet cherry)	<i>P. Cerasus</i> (4x) (sour cherry).
	<i>P. persica</i> (peach)	<i>P. domestica</i> (6x) (plum).
	<i>P. Amygdalus</i> (almond)	<i>P. Laurocerasus</i> (22x) (cherry laurel).
7	<i>Rubus Idaeus</i> (raspberry)	<i>R. "Himalaya Berry"</i> (4x).
	<i>R. rusticanus</i> (blackberry)	<i>R. "Veitchberry"</i> (4x).
7		<i>R. "Loganberry"</i> (6x).
		<i>R. "Mahdi"</i> (3x).
		<i>R. "Laxtonberry"</i> (7x).
	<i>Fragaria vesca</i> (wood strawberry)	<i>F. elatior</i> (6x).
	<i>F. americana</i>	<i>F. chiloensis</i> (8x).
		<i>F. virginiana</i> (8x).
		All cultivated vars. (8x).
	<i>Rosa moschata</i> (musk rose)	<i>R. damascena</i> (3x, 4x, 5x) (attar rose).
	<i>R. chinensis</i> var. old pink china	<i>R. odorata</i> Gloire de Dijon (4x).
	<i>R. macrophylla</i>	<i>R. chinensis</i> Bengal Rose (4x and 5x).
7		<i>R. macrophylla</i> var. <i>Korolkowii</i> (4x).
		<i>R. pimpinellifolia</i> (4x).
8		<i>R. rubiginosa</i> (5x) (sweet briar).
	<i>R. cinnamomea</i> (cinnamon rose)	<i>R. cinnamomea</i> vars.
8	<i>Medicago lupulina</i> (black medick)	Penzance sweet briars (6x).
8	<i>Trifolium repens</i> (wild white clover)	<i>R. Moyesii</i> (6x).
9		<i>M. sativa</i> (4x) (lucerne, alfalfa)
	<i>Citrus Limonum</i> (lemon)	<i>T. repens</i> var. <i>giganteum</i> (4x) (Dutch white clover).
	<i>C. sinensis</i> (Valencia orange)	<i>Fortunella Hindsii</i> (Chinese kumquat).
	<i>C. nobilis</i> (tangerine)	<i>C. sinensis</i> seedling (4x).
20	<i>C. grandis</i> (grape fruit) (often partially apogamous on selfing and crossing)	
	<i>Aesculus Hippocastanum</i> (horse chestnut)	<i>A. carnea</i> (4x).
19	<i>A. Pavia</i>	
	<i>Vitis</i> spp. and	<i>Vitis</i>
19	Grape vine, vars. Muscat	Grape vine, vars. Muscat gigas (4x).
	Sultanina	Sultaninagigas (4x).

x.	Diploid Forms.	Polyploid Forms.
13	{ <i>Gossypium arboreum</i> <i>G. indicum</i> (Indian and Chinese cotton)	<i>G. barbadense</i> (4x). <i>G. hirsutum</i> (4x) (American and Sea Island cotton).
12	<i>Viola</i> spp.	Garden "pansies" (4x).
11	{ <i>Fuchsia fulgens</i> <i>F. splendens</i>	<i>F. triphylla</i> (3x). <i>F. coccinea</i> (4x).
		Large-flowered vars. (8x).
9	<i>Primula elatior</i> (cowslip)	<i>P. Auricula</i> (6x).
8	<i>Aucuba chinensis</i>	<i>A. japonica</i> (4x).
14	<i>Cyclamen coum</i>	<i>C. persicum</i> var. (6x).
12	<i>Solanum Lycopersicum</i> (tomato)	<i>S. Commersonii</i> (3x).
		<i>S. caryocarpum</i> (3x).
		<i>S. medians</i> (3x).
		<i>S. "tuberosum"</i> (3x, 4x) (potato).
		<i>S. demissum</i> (4x, 5x).
		<i>S. nigrum</i> (6x) (black nightshade).
		<i>C. s.</i> var. <i>grandiflora</i> (6x).
7	<i>Cucumis sativus</i> (cucumber)	<i>C. maxima</i> (4x).
12	<i>Cucumis Melo</i> (melon)	<i>C. Pepo</i> (6x).
17	<i>Campanula carpatica</i>	<i>C. rapunculoides</i> var. <i>grandiflora</i> (6x).
7	<i>Lobelia</i> spp.	<i>L. Erinus</i> vars. (6x).
16	{ <i>Dahlia coronata</i> <i>D. coccinea</i>	<i>Dahlia variabilis</i> (4x).
9	<i>Chrysanthemum segetum</i>	<i>Chrysanthemum indicum</i> , hort. vars. (6x, 10x, etc.).

be made to lists of chromosome numbers published by Gaiser,¹ and Tischler.²

These results show that many of the most important modern improvements in cultivated plants are due to polyploidy. But they do not show any simple rule for obtaining new cultivated plants of value. Many of the most important crop plants, such as maize, barley and peas, are diploids. On the other hand, many polyploid species are less useful than their diploid relatives; they may even be, like the sour cherries, relatively dwarf. Where the best cultivated forms are polyploid, it is often found that their wild relatives have the same chromosome number. The wild forms of tuberous *Solanum* growing in the Andes are tetraploid, just like the best cultivated potatoes. The wild Chilean strawberry is octoploid, just like the best culti-

¹ *Bibliographia Genetica*, 6, 171-466.

² *Tabulae Biologicae Periodicae*, 1 (1930).

vated strawberries of Europe. How do these results agree with our experiments? The answer is now fairly clear.

When a polyploid species arises in nature in the way in which *Primula kewensis* or *Raphanus-Brassica* arose (and from what we have seen this is evidently the method) it reproduces its like, subject to natural selection. It varies, and those of its offspring which are best adapted to natural conditions survive. There is no general reason why a new form should be better fitted to survive when it is larger than its parents than when it is smaller. Where the parental species differ in size, as they usually do, it will be possible for new forms to vary by the segregation of parental size differences just as *Primula kewensis* does in the segregation of mealiness. Such segregation has actually been found in *Primula kewensis*, *Nicotiana* and *Digitalis*. Dwarf seedlings may appear in the second generation. In short, the new type will survive in a form larger or smaller than its parents quite independently of the fact that it started in the first generation as a giant. In such species as the sour cherry, *Prunus Cerasus* ($4x$), and the black nightshade, *Solanum nigrum* ($6x$), the polyploid has taken a dwarf type as compared with its diploid relatives.

This reversion to the dwarfer type does not necessarily affect all the organs of the plant equally. For example, Erlanson, 1931¹ has found in the North American roses that the diploids are more robust than the related polyploid forms, but the pollen-grains are larger in the polyploids. European dog-roses of the "Caninae" group, studied by Täckholm (1922),² are different. They are chiefly pentaploids and have not varied by segregation since their origin. They have retained the

¹ *Genetics*, 16.

² *Acta Horti Bergiana*, 7, 97-381.

characteristic gigantism of the first generation which distinguishes them from normally seed-producing polyploids of similar age. This is probably due to a special device by which they produce haploid pollen grains and tetraploid egg-cells; the extra three sets of the latter never pair and therefore never change through segregation.

Again, in many cases it has been found difficult to

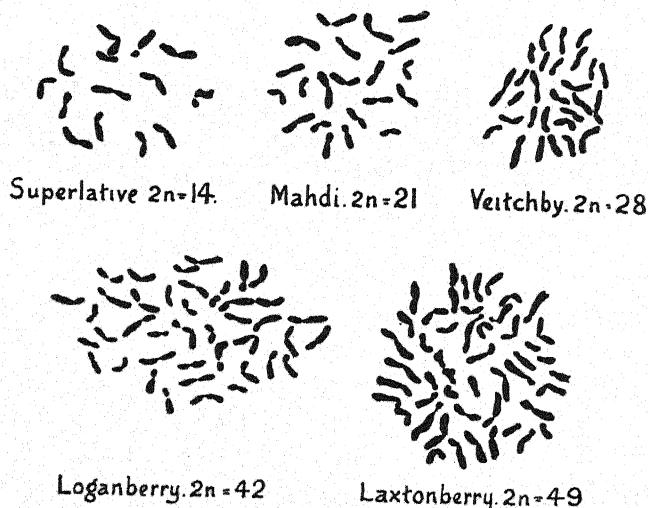


FIG. 21.—THE CHROMOSOME COMPLEMENTS OF SIX FORMS OF *RUBUS* (BLACKBERRY AND RASPBERRY).

The diploid "Superlative" is a variety of raspberry. (From Crane and Darlington, 1927, *Genetica*, 9.)

distinguish between related diploid and polyploid species, although we know from experience that they would be inter-sterile or yield sterile progeny when crossed, and it is therefore undoubtedly useful to separate them. This is the case with the tetraploid and 16-ploid forms of *Silene ciliata* (Blackburn, 1927¹), with the diploid *Solanum Caldasii*, sometimes confused with the tetraploid *S. palustre* (Rybin, 1929²), and with the diploid

¹ *Proc. Fifth Int. Cong. Genet.*, Berlin.

² *Bull. App. Bot.*, 19.

Japanese plums of the *triflora-Simonii* group which have been confused with the hexaploid European plums (*P. domestica* and *P. insititia*). Similarly, the diploid Iceland poppy, *Papaver nudicaule*, has a decaploid variety, *striatocarpum* (Ljungdahl, 1924¹), and Peto has found diploid and tetraploid forms of *Agropyrum cristatum* which are very nearly indistinguishable (1930),² and of *A. Smithii* var. *molle*, which are altogether indistinguishable.

Where, on the other hand, polyploidy has occurred in cultivated forms, man has been able to preserve the new types that he wanted. This is probably the story of bread wheat, *Triticum vulgare*, the plum, *Prunus domestica*, the potato, *Solanum tuberosum*, and *Dahlia variabilis*, the source of our important cultivated Dahlias (Lawrence, 1929³). It is almost certainly the story of the American Timothy, *Phleum pratense*, the red Chestnut, *Aesculus carnea*, and of our best garden varieties of tulips, hyacinths, irises, fuchsias, pansies, chrysanthemums, strawberries and blackberries. In some of these cases hybridisation in the remote past has doubtless taken place. We can only guess what the parents of such polyploids as the plum and the bread wheat may be; indeed, a great deal of guessing has been done without much danger of contradiction. But we can see that in the bread wheat (*Triticum vulgare*) and in the cultivated oat (*Avena sativa*), which are both hexaploid, the gigantism of the original forms has been preserved, where it was useful, in the plants as a whole as well as in particular organs. The pollen-grains, as in the roses, are roughly proportional in size to the number of chromosome sets present (Sax, 1922⁴).

¹ *Sv. Bot. Tidskr.*, 18.

² *Can. J. Research.*, 3.

³ *J. Genet.*, 21, 125-59.

⁴ *Genetics*, 6.

The diploid ancestors of the bread wheat and the plum have disappeared. Their chromosome sets have altered since they joined together to make the polyploid. Little hope is there then of tracing them from analysis of the polyploid. But in other cases we are on safer ground. The circumstances in which some of the polyploids first appeared are known. It is known that the large-flowered fuchsias with high chromosome numbers (Warth, 1925¹), appeared for the first time in the middle of the last century, after the introduction of new species with low chromosome numbers from Mexico, Peru and elsewhere. And it is known that the form *Aesculus carnea* appears frequently in gardens, is intermediate between *Aesculus Hippocastanum* and *A. Pavia*, and has a chromosome complement which can be recognised as the sum of the complements of these two species, for one species has smaller chromosomes than the other (Skovsted, 1929²).

One case, the loganberry, was very much of a riddle before its chromosome complement was studied (Crane and Darlington, 1927³). The loganberry appeared in a garden in California, and was supposed to be a hybrid between a blackberry and a raspberry. But it resembled the blackberry parent much more closely than the raspberry. It bred approximately true and was highly fertile so that the story of its origin was doubted. The loganberry proved to be a hexaploid, and there can be little doubt but that it arose as a cross between a tetraploid blackberry and a diploid raspberry in which doubling of the chromosome number had occurred. The six sets of the loganberry may be represented: $RRB_1B_1B_2B_2$.

¹ *Zeits. ind. Abst. Vererb.*, 38.

² *Hereditas*, 12, 64-70.

³ *Genetica*, 9.

When the loganberry breeds it produces a proportion of seedlings like itself, but most of the progeny differ conspicuously by a reduction in fertility (see Fig. 22). This is shown clearly by the size of the fruits seen in the illustration. Again, we are dealing with the same kind

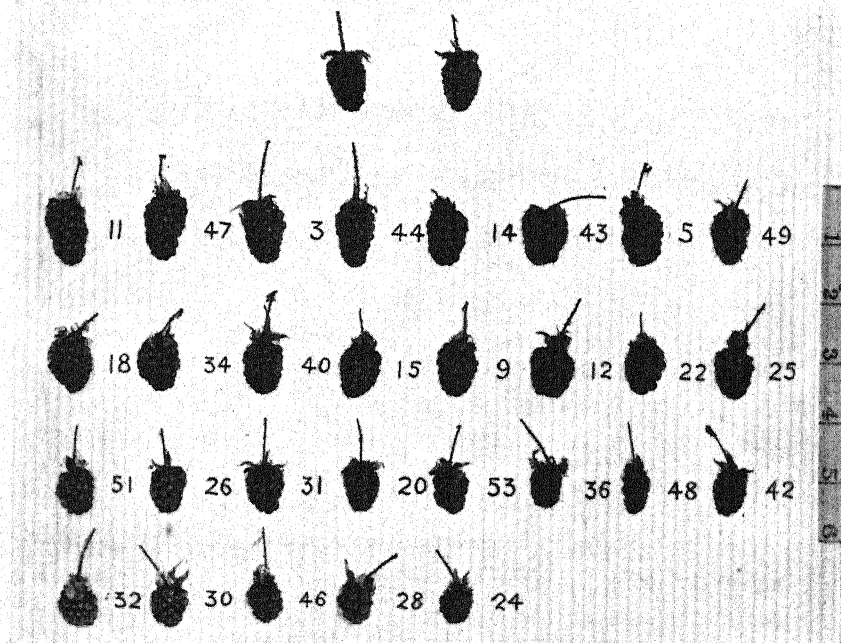


FIG. 22.—FRUITS OF THE LOGANBERRY.

Fruits of the loganberry, and of twenty-nine of its self-fertilised seedlings showing the loss of fertility as a result of slight segregation in a hybrid with doubled chromosome number. (From Crane and Darlington, 1927, *Genetica*, 9.)

of segregation as that found in *Primula kewensis*, following, in this case, the occasional pairing of raspberry and blackberry chromosomes. The new combinations are naturally less fertile than the original product of doubling, in which each chromosome has an identical mate and the whole complement is balanced.

The loganberry has been crossed back with diploid raspberries by Messrs. Laxton. Usually, it has given tetraploid seedlings as would be expected, thus: $RR B_1 B_1 B_2 B_2 \times RR = RR B_1 B_2$. These seedlings are sterile because B_1 is unlike B_2 just as f is unlike v in *Primula kewensis*. An exceptional seedling appeared more like the loganberry parent than usual. This seedling, the "Laxtonberry," had seven sets of chromosomes ($2n = 49$). Evidently an unreduced ($6x$) egg-cell of the loganberry had been fertilised by a reduced (x) pollen grain of the raspberry. This seedling was less fertile than the loganberry presumably on account of its odd raspberry set, which had nothing to pair with and was distributed irregularly to the germ-cells (Crane and Darlington, *l.c.*).

Gregor and Sansome (1930),¹ have produced a hexaploid timothy grass by crossing diploid and tetraploid species. The triploid F_1 gave unreduced germ-cells. The result is analogous with the loganberry; it is fertile, giant and intermediate, with a leaning in the direction of the tetraploid parent species. There can be no doubt that the hexaploid giant timothy grass of the United States arose in this way; the circumstances of its origin are not recorded, but its resemblance to the artificial hybrid is unmistakable.

Müntzing's hybrid² referred to in the table in the last chapter is an example of the artificial production of a new form indistinguishable from a wild Linnean species, *Galeopsis Tetrabit*, the hemp nettle, by crossing two related species of smaller stature. Such crossing occurs in nature, and we may consider this as definitely showing how this species arose and as a confirmation of our view (based on considerations

¹ *J. Genet.*, 22.

² *Hereditas*, 14, 153-72.

of fertility and chromosome behaviour at reduction) that seed-fertile polyploid species are usually of hybrid origin.

The evidence of the origin of yet a third species has been discovered by Huskins (1930).¹ Fifty years ago a new species of grass, *Spartina Townshendii*, made its appearance on the shores of Southampton Water. Its vigorous growth has since made it important in many countries as a means of land reclamation. It is intermediate in form between two old species *S. alterniflora* and *S. stricta*. Huskins has shown that these latter have respectively fifty-six and seventy chromosomes; the new species has 126 chromosomes.

The experiments with hybrid polyploids therefore show how a great number of important cultivated species and varieties have arisen, viz., by hybridisation followed by chromosome doubling. When therefore anyone raises a hybrid which proves to be highly sterile, he now knows that, unless its sterility is due to the malformation of the flowers, there is some hope of finding that the exceptional seedling to be raised from it will be of special value in horticulture; it will be fertile, true-breeding and giant.

Of less general importance are those polyploid varieties which have arisen in cultivation without hybridisation, such as the giant *Primula sinensis*, *Oenothera Lamarckiana*, and *Campanula* Telham Beauty. Recent additions to this type are tetraploid giant grape varieties cultivated in California (Nebel, 1929²), and the triploid oranges and apples to be referred to later.

In *Tulipa*, two species seem to be of this type. *T. Whittallii* is a larger form of *T. Hageri* and *T. sylvestris* of *T. australis*. Both of the giant species are tetraploid,

¹ *Genetica*, 13.

² *Die Gartenbauwissenschaft*, 1, 349-92.

their relatives diploid. Sir Daniel Hall has suggested ¹ that *T. sylvestris* has probably arisen independently, by doubling of the chromosome number, from *T. australis* on many occasions and in different localities. Like the other non-hybrid tetraploids these species are infertile.

¹ *Book of the Tulip*, 1929.

CHAPTER XIII

BREEDING WITH POLYPLOIDS

CYTOLOGICAL study of polyploid species shows why most of them behave in breeding like the hybrid polyploid of the *Primula kewensis* type. Whether they are tetraploids, hexaploids or octoploids, their chromosomes usually unite in pairs at reduction. This rule is particularly strict in those plants which depend on seed fertility for their reproduction, *e.g.*, the cereals. In these the differentiation is sharper even than in *Primula kewensis*. It is more like that in the *Raphanus-Brassica* tetraploid, where no pairing takes place between corresponding chromosomes of the two species even in the diploid hybrid (Fig. 17). They are, as it were, in two watertight compartments. The species behave on self-fertilisation almost exactly as though they were diploids. Yet, apart from their chromosome numbers, there are three ways in which these species show us that they are polyploids.

In the first place, a particular character in a polyploid may be given by the presence of any one of several different factors. These factors are probably in corresponding chromosomes of the different diploid ancestors of the polyploid. For example, in the hexaploid bread wheat, *Triticum vulgare*, Nilsson-Ehle found that some varieties may have three independent factors affecting the red colour of the grain. In the hexaploid oats, Åkerman found similar factors affecting the presence

of green leaf-colour. Other characters are affected by two factors. We do not know that these multiple factors are due to the plant being a polyploid, but since they are not usually found in diploid plants, it is very probable.

The occurrence of two independent factors for black grain-colour has been turned to advantage in breeding oats in Sweden. Old black varieties of oats had a single factor which may be called B_1B_1 for black colour. These varieties used to sport so as to give a hundred or so white grains in every bushel, owing to the corresponding chromosomes in the second set carrying the recessive factor b , and occasional pairing taking place between the B and b chromosomes. The white grains, of course, reduced the value of the oats by giving it unfairly an appearance of impurity. Åkerman¹ therefore crossed two black varieties, one of which was $B_1B_1b_2b_2$, and the other $b_1b_1B_2B_2$ (*i.e.* black by virtue of the other factor), and from the F_2 a new type doubly black $B_1B_1B_2B_2$ was raised, which never sports to white seeds.

Secondly, when diploid species are X-rayed their offspring change in every direction; polyploids do not vary anything like so much as their diploid relatives. In fact, Stadler (1929)² found that, while tetraploid species of oats and wheat did mutate a little under the same doses as gave big changes in the diploids, the hexaploid bread wheat and cultivated oats showed no change whatever. What is true of change induced by X-rays is probably equally true of natural change. The extra chromosome sets act as a buffer against the effects of changes in the chromosomes, so that in poly-

¹ *Sveriges Utsädesför. Tidskr.*, 34, 4-20 (1924).

² *Proc. Nat. Acad. Sci.*, 15, 876-81.

ploids we can have very little idea of what is going on inside the chromosomes, as compared with diploids. The doubly black-seeded variety of oats is an example of this; the second pair of factors is there for safety and if mutation of B_1 to b_1 occurs, we shall not notice it.

But we can occasionally see the results of other changes, which provide a third kind of evidence of polyploidy. Diploid pure lines sometimes breed true, and for generations show no variation to the closest scrutiny: such are known in the *Triticum monococcum*, of de Vilmorin, which has bred true for eighty years, and in Johanssen's pure lines of broad bean, *Vicia Faba*. But the hexaploid cereals cannot be depended upon. Awnless cultivated oats of as pure race as can be got always throw a proportion—varying with the variety and particularly high in new varieties—of individuals having awns on their flowering glumes. And when these are selfed, their progeny (which will appear in cultivation unless oats for seed are severely rogued) are of quite a distinct and inferior type, indistinguishable, in fact, from the wild oat, *Avena fatua*. These are called "fatuoid" oats. They are characterised by having both the spikelets provided with a twisted, kneed awn, and each grain marked by a prominent articulation surrounded by a tuft of hairs (Fig. 23).

Huskins (1927)¹ has shown from the chromosome behaviour at reduction that the "mutants" are due to the same cause as the appearance of the mealy offspring of *P. kewensis*, which also resemble a related species, *P. verticillata*. In both species of *Avena*, *A. fatua* and *A. sativa* each chromosome type is represented by three pairs. Taking two of these pairs we may consider that *A. fatua* has the constitution FF,FF, while *A.*

¹ *J. Genet.*, 18, 315-64.

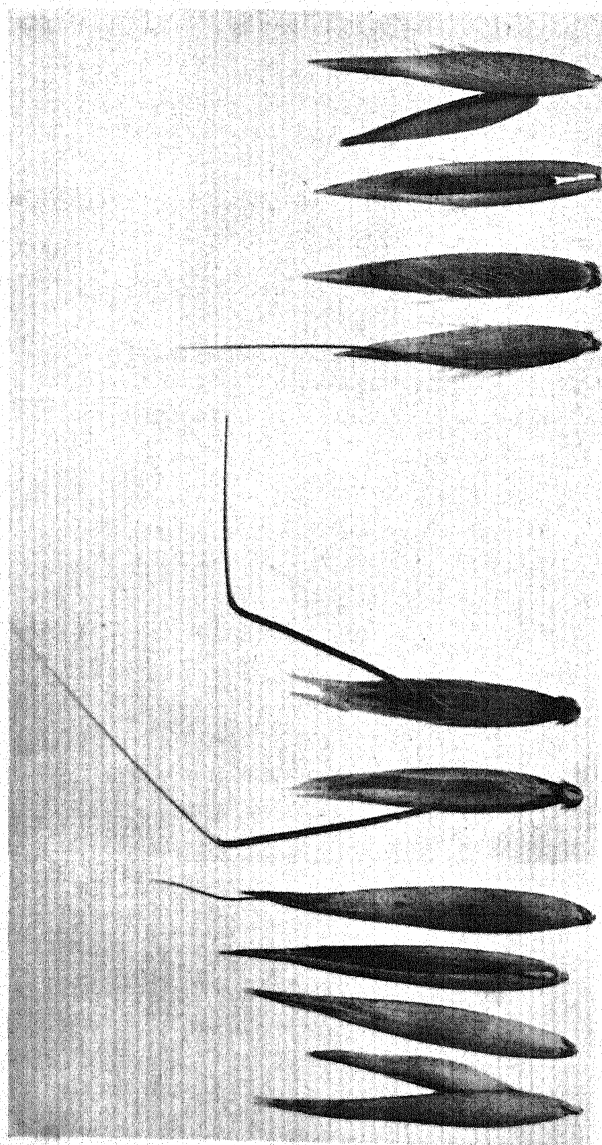


FIG. 23.—SPIKELETS OF OATS: LEFT, *AVENA SATIVA*; CENTRE, *AVENA FATUA*; RIGHT, F_1 HYBRIDS.

[Reproduced by kind permission of Mr. J. Philp.]

The F_1 hybrid is indistinguishable from the heterozygous "fatuoid" seed sport; *A. fatua* is indistinguishable from the homozygous fatuoid.

sativa has the constitution FF,ff , and regularly produces gametes Ff which reproduce it truly. Both, as a rule, breed true, but occasionally in *A. sativa* (particularly in new varieties which have been disturbed by hybridisation) F pairs with f , or the four chromosomes $FFff$ form a ring at reduction. The result is the formation of germ-cells that are FF or ff instead of the normal Ff . When these meet the normal germ-cell the result is the production of two new types— $FFFf$ and $Ffff$. The first of these is our slightly awned type, which when selfed gives, together with the normal and its own type, the pure fatuoid, $FFFF$, in the proportions 1:2:1. The same result is given by the first cross between the wild oat and cultivated oat, so that we know in this case roughly what makes the difference between the two.

This property of giving away its hybrid origin is probably very common in new polyploid species, for the bread wheats do just the same thing. They throw a sport called a "speltoid" in exactly the same way as the oats throw a fatuoid. Again, this form resembles a related species, *Triticum Spelta*, in the character of its spike and grain (Huskins, 1928¹).

Such behaviour shows that rogueing is a much more serious business with polyploids than with diploids. All the materials are there for them to produce a whole array of sports, and if they are left to themselves although they are continually self-fertilised they will none the less gradually become more and more adulterated by their own throw-backs, which will mainly be of a character unwanted in cultivation.

¹ *J. Genet.*, 19.

CHAPTER XIV

CROSSING POLYPLOID SPECIES

If this is the way polyploid species behave when they are continually inbred, something rather complicated is to be expected when they are crossed. Diploid species-crosses very often give sterile hybrids. Polyploid species, if they have the same number of chromosomes, cross more often to give fertile hybrids. Polyploid species are therefore often more difficult to separate than diploid. Since it is not known how the polyploid species themselves are made up (except that they are hybrid), it cannot be predicted how they will behave when they are bred together; the same combination may be broken up in many different ways.

One of the exceptional results they give is what Engledow (1923)¹ has called "shift." In the offspring of a cross between *Triticum polonicum* and *T. durum* he found no segregation of the long-glume character of the Polish wheat. All the progeny for several generations remained intermediate in character. In the same way, in a cross between a rough-chaffed rivet wheat, *T. turgidum*, and *T. polonicum*, Biffen never recovered the grey chaff colour on the rivet, although progeny were grown to the number of 100,000. The same suppression of a character by crossing has been found by Backhouse (1918),² and Vavilov in the tetraploid cereals, and in other cases they have found the reverse effect of a character being accentuated. All

¹ *J. Genet.*, 13.

² *Ibid.*, 7.

these results are due to the new hybrids breeding true to certain of their new combinations of factors. The long-glume of Polish wheat may be supposed to depend on characters carried in two pairs of chromosomes, P_1P_1 and P_2P_2 , while the corresponding chromosomes of *T. durum* are p_1p_1 and p_2p_2 . Then the hybrid will be of the composition $P_1P_2p_1p_2$, and if P_1 pairs with P_2 and p_1 with p_2 we shall get no germ-cells except with one P and one p . We shall never get back the P_1P_2 or the p_1p_2 type, any more than we get back *Primula floribunda* and *Primula verticillata* from the hybrid *P. kewensis* (Darlington, 1928¹). These new hybrids therefore produce new forms just as much as diploid hybrids, but they are fertile and more constant. Let us see what use has been made of this in improving cultivated plants.

Take the case of the cultivated strawberry, whose history have been well described by Bunyard² and Pearl.³ The wood strawberry, *Fragaria vesca*, was cultivated for its fruits in the fifteenth century. It produced no variations of importance, except an ever-flowering "alpine strawberry" analogous to the "All Saints" cherry and the "Lloyd George" raspberry. The fruits always remained small. This species is diploid. Another species that came into cultivation at this time in France and England was *Fragaria elatior*, the Hautbois strawberry, also a native of Europe. This species differs from the former in holding its ripe fruits above the leaves, and in the musky flavour of the fruits. Like the wood strawberry, it has small fruits, and although still occasionally grown, it likewise has shown no considerable improvement in size in the course of four hundred years of cultivation. This species is usually dioecious, having male and

¹ *J. Genet.*, 19.

² *J. Roy. Hort. Soc.*, 39.

³ Leaflet, South-Eastern Agric. College, 1928.

female flowers on different plants. *F. elatior* is hexaploid, and therefore will not yield fertile hybrids with *F. vesca*.

In the seventeenth century, the scarlet strawberry, *F. virginiana*, from North America was introduced by John Tradescant. The plant was distinct in vegetative characters and its fruit was different in shape and flavour from that of the two European species, but it was scarcely any bigger, about half-an-inch long. It produced more varieties than the older strawberries, but no marked improvement. This species is octoploid and does not cross with either of the first two.

The last important species to be introduced to Europe was the South American *F. chiloensis*, which came to France in 1712. But the plants introduced were all females, and consequently set no seeds until planted near other species with pollen. *F. chiloensis*—very distinct from the others, having stout scapes with few flowers, and fruits twice their size—is octoploid. From all accounts it is certain that the few plants of it that were introduced afforded the first possibility of raising the large-sized fruits familiar in our modern cultivated varieties. But since the plants were female, it is evident that the first varieties to occur in cultivation were the results of natural crossing with other species. All the modern large-fruited varieties examined are octoploid, and it is quite clear that they arose from crossing with the other octoploid species, *F. virginiana*.

Great numbers of improvements, like this in strawberries, have been found to occur following the introduction of species into cultivation, and they have always been attributed to cultivation. If "cultivation" means "opportunity for hybridisation," the popular idea is correct. No other effect of cultivation has ever been shown to have any importance in plant improvement.

It is curious that in spite of improved varieties of strawberries being raised from crossing, they were not sufficiently improved to suggest the advantage of further crossing. The only crosses, as we have seen, were accidental. In fact, we may say they could hardly have been helped. It was only a hundred years later, with the fashion set by Knight in England of raising plants from seeds, that new strawberry seedlings appeared. Soon after, by systematic crossing of the derivatives of these early seedlings, Laxton produced the first strawberries having the qualities required in cultivation to-day.

The same kind of change is undoubtedly responsible for the improvement of the Chilean wild potato. But here part of the improvement was probably carried out by the natives in South America before introduction into Europe, and only part after.

In this way it is clear that almost as rapid improvement can be made by crossing polyploid species with the same chromosome numbers as by crossing diploids and raising polyploids from them. The result, too, will not depend on chance, for polyploidy is there to start with. When two tetraploid species are crossed, four different chromosome complements originally derived from four different species are thrown into the melting pot. Not only is the result often fertile, which might well not be, were the parents diploid, but an enormously increased number of combinations can be made from the sorting out of the chromosomes derived from the four ancestral species. Among these combinations the breeder can select the new and improved forms that he wants, and propagate them vegetatively as in the case of strawberries and potatoes; or, by inbreeding, he can extract new strains that will breed true, as in the cereals.

CHAPTER XV

STERILITY IN POLYPLOIDS: TRIPLOIDY

So far, we have dealt chiefly with examples in which polyploidy has given advantageous results, but we must now mention some of the difficulties that polyploids offer to the breeder—difficulties which may, however, be guarded against by reference to a list of chromosome numbers.

When polyploids with the same numbers of chromosomes are crossed, the result is a hybrid which, as a rule, is of moderate fertility; but when their chromosome numbers are different, difficulties are to be expected at reduction with consequent loss of fertility. Take the case of a cross between a diploid with a single set of chromosomes in its gametes (like *Prunus cerasifera*, the myrobalan plum) and a hexaploid with three sets (like the "Jefferson" variety of *P. domestica*), such as that made by Crane.¹ Irregularities of reduction might be expected. But four chromosome sets are brought together in the hybrid just as in the cross between *Triticum durum* ($4x$) and *T. polonicum* ($4x$). Three of these are derived from one parent and one from the other, instead of two from each. Does this matter, since in any case the four sets are originally derived from four different species? So far as behaviour of the chromosomes is concerned it certainly does not. The

¹ Cf. Darlington, 1930, *J. Genet.*, 22, 65-93.

hybrid behaves just like any other tetraploid and even gives seedlings when back-crossed with the hexaploid plum parent (Crane, unpublished). The same kind of result has been achieved in *Papaver*, *Crepis* and *Digitalis* hybrids.

This is well enough where there is an even number of sets of chromosomes in the hybrid, but where the number is odd, reduction can never be regular; chromosomes of the odd set have nothing corresponding to pair with, and they pass at random to one pole or the other. The result is the production of germ-cells with all kinds of chromosome numbers, and we know from other instances with odd chromosomes what this means. Here the case is worse, for a triploid ornamental cherry like *Prunus avium* var. *nana* (a cross between the diploid sweet cherry and the tetraploid sour cherry) has eight extra chromosomes. It produces germ-cells with every number between eight and sixteen, and among these the balanced ones with eight and sixteen only come once in over a hundred times. The result is that such a triploid is highly infertile.

This, however, has its uses. The triploid water-cress is sterile. It is eaten in winter and possibly is sturdier on account of its seed-sterility (Manton, unpublished). The cherry in question is an ornamental variety, and if the cherries of the Japanese group (e.g., *Prunus serrulata* and *P. subhirtella*) are examined, it is found that nearly all of them are either triploid or double-flowered. Both these types are sterile. Clearly, gardeners have chosen for ornamental purposes those varieties which produce least fruit, for in trees which are grown for a display of flowers, fruit is often a disadvantage. Therefore, if one is raising ornamental trees which can be propagated readily by cuttings or grafts,



tetraploids should be crossed with diploids to get, not merely something new, but also something with the advantage of sterility. Actually the triploid Japanese cherries have arisen accidentally, and not by design. Their sterility depends simply on the presence of an odd set which has been introduced without hybridisation; the odd set is the result of a germ-cell with the unreduced diploid number on one side fusing with a haploid germ-cell on the other.

This is what has happened in the garden tulips. Several important varieties such as Keizerskroon, Massenet, Pottelbakker and Pink Beauty, are triploid. They arose from the fusion of a diploid egg with a haploid pollen grain. Consequently, unlike the products of hybridisation with non-giant tetraploid species, such triploids usually show a suggestion of gigantism which has led to their selection. This is best exemplified by the hyacinths, but it must be pointed out that the hyacinths are altogether exceptional in not being badly affected by having odd chromosome numbers. Therefore their triploids are not sterile, but give rise to seedlings having various numbers, which, although less vigorous than the triploids themselves, are occasionally worth growing. The best varieties of garden hyacinths are triploids (de Mol, 1921¹). The first to appear was Grand Maître in 1870. They are all larger in bulb and flower than either the diploids which preceded them or the odd-numbered forms to which they have given rise as seedlings. They proliferate freely, their bulbils maturing in four years, that is more rapidly than those of the diploids.

The following list gives some idea of the composition of modern varieties of hyacinths.

¹ *Arch. Neerl. d. Sci.* 3 B.

General Pélisseur	} diploid, $2n = 16$.
Roi des Belges	
Nimrod	$2n = 19$.
Rosea maxima	$2n = 20$.
van Speyk	$2n = 21$.
l'Ordre Parfait	$2n = 22$.
City of Haarlem	$2n = 23$.
Grand Maître	
Generaal de Wet	
King of the Blues	} triploid, $2n = 24$.
Queen of the Pinks	
Lord Balfour	
Lady Derby	
l'Innocence	
Cardinal Wiseman	} $2n = 27$.
Garrick	
la Grandesse	} $2n = 28$.
Totilla	$2n = 30$.

On account of their inability to breed true, triploids and other odd-numbered polyploids are naturally confined in horticulture and in nature to species that are propagated vegetatively, such as potatoes, tulips, hyacinths, irises, cannas, spiderworts and day lilies. Many triploids and pentaploids have by purely vegetative means gained for themselves sufficient distribution to be reckoned as species. Such are *Ochna serrulata*, the wild pear of Natal, and *Rosa* and *Hieracium* species, the tuberous *Solanum Commersonii* and the bulb-forming *Tulipa Clusiana* and *T. saxatilis*. There are occasional triploids which are propagated for fruit production. In *Rubus*, for example, the Mahdi is a triploid hybrid with two sets from a tetraploid raspberry and one from its blackberry parent. The same cross has given the tetraploid veitchberry owing to the blackberry set having doubled, or rather failed to reduce in forming its germ-cells. While the veitchberry is highly fertile, the Mahdi is so infertile as to be merely a horticultural curiosity (Fig. 24).

The veitchberry happens to be male-sterile, but this abnormality must not be confused with generational sterility. It is merely a structural deformity in the anthers which has been found to occur in seedlings of



[Reproduced by kind permission of Mr. M. B. Crane.]
FIG. 24.—HYBRIDS BETWEEN NOVEMBER ABUNDANCE RASPBERRY ($4x$) AND *RUBUS RUSTICANUS* ($2x$).

Left, the Mahdi, a sterile triploid ($3x$); right, the veitchberry, a fertile tetraploid ($4x$). These hybrids are strictly comparable with those illustrated in Fig. 18 in regard to their origin.

well-known raspberry varieties such as Superlative (Crane and Lawrence, 1929¹). Such varieties are heterozygous in the factor for male-sterility, and no

¹ *J. of Pomology*, 7, 276-301.

doubt the male-sterility of the veitchberry is derived from its raspberry parent. This deformity, as the figure shows, has no ill effect on seed fertility if pollen is provided from elsewhere. The Mahdi, on the other hand, being triploid, is incapable of setting complete fruits, although of the same parentage and not male sterile.

It is plain that with plums, cherries and blackberries fertility in fruit production is directly concerned with seed formation. The size of a blackberry is directly proportional to the number of drupels set, although, of course, the size of the individual drupels varies in different races and species (Crane and Lawrence, 1930¹). But in pears and apples it is quite another story. Here there are ten seeds in each fruit, and it is possible to get the fruit developed when only one of the ten grows. It is even possible to have fruits without any good seeds at all. It follows that triploid apples and pears have some chance of success in cultivation, for only one seed in a hundred needs to grow to give one fruit in ten set—that is, quite a good crop. It is therefore not surprising to find that many of our best varieties are triploids, as the following list shows :—

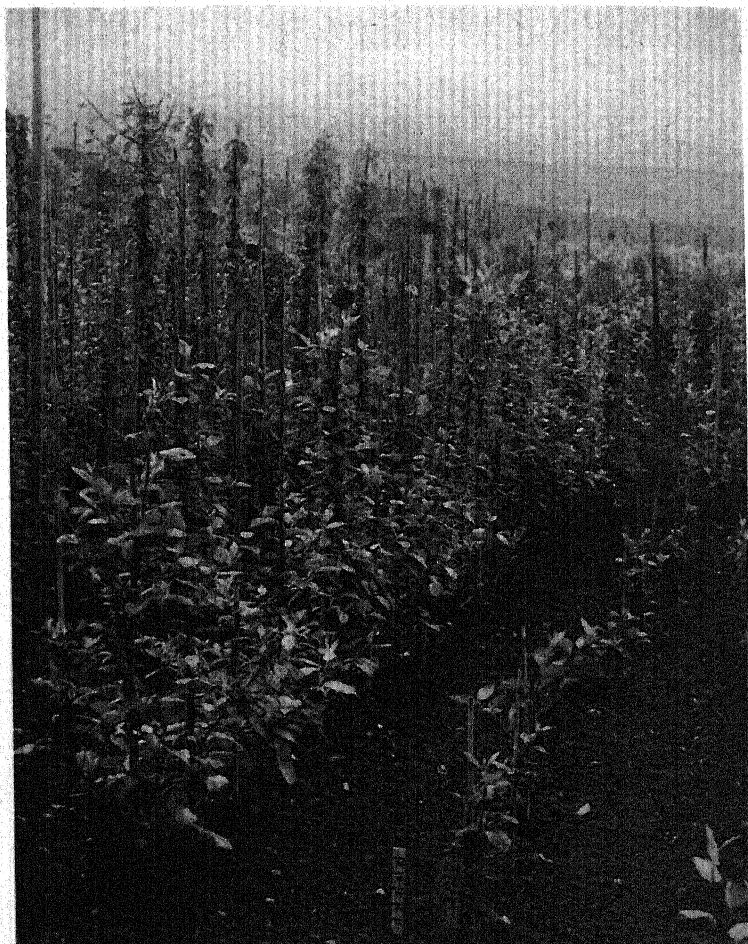
APPLES.

*Diploid, thirty-four
chromosomes.*

Lord Derby.
Beauty of Bath.
Lane's Prince Albert.
Newton Wonder.
Cox's Orange Pippin.
Worcester Pearmain.
Northern Spy.

*Triploid, fifty-one
chromosomes.*

Bramley's Seedling.
Blenheim Pippin.
Warner's King.
Baldwin.
Ribston Pippin.
Genet Moyle.
Gravenstein.



[Reproduced by kind permission of Mr. M. B. Crane.]

FIG. 25.—SEEDLINGS OF APPLES, THREE YEARS OLD.
Left, from diploid varieties intercrossed; right, from diploid varieties crossed
with triploids.

PEARS.

Fondante de Thirriot.
Beurré Hardy.
Doyenné du Comice.
Williams's Bon Chrétien.

Beurré Diel.
Conseiller à la Cour.

These triploids arise not by crossing but, as with the cherries, hyacinths and tulips, through an unreduced germ-cell being effective in fertilisation. Their advantage is therefore not in any new qualities that are brought together, but in the different scope for variation where three sets of chromosomes are present, and in the increased vigour of growth that is found in these varieties.

But the breeder must beware of following traditional method and using these excellent varieties for producing new improvements. He may well expect (if he is unaware of the chromosome conditions which lead to their vigour) that the more vigorous varieties will give the most vigorous seedlings, and breeders have expressed their surprise that this is not so.¹ The stronger varieties give regularly weaker seedlings than the weaker (diploid) varieties (Crane and Lawrence, *loc. cit.*). The triploid is good enough for fruit production among apples, but its irregular reduction is as fatal as ever for any breeding work, and to raise a good new variety by crossing with a triploid is an ungrateful task. Diploids must be crossed together, and from them all the best results can be obtained; their seedlings are diploid with an occasional triploid. But triploids do not give a tenth as many seedlings, and those they do give are all of poor growth, usually distorted and unhealthy looking. The same is probably true in the case of hyacinths. The easiest way of getting good new triploid varieties would be by breeding diploids, not by breeding the better triploid varieties.

¹ Hatton, Masters Memorial Lecture, Roy. Hort. Soc., 1930.

CHAPTER XVI

SECONDARY POLYPLOIDY

THE apple and pear group offer another interesting peculiarity in their chromosome properties, and therefore in their inheritance. It will be seen that the basic number 17 is not paralleled in any of the other examples that have been given. The question arises, Is this really a basic number, or does it conceal the evidence of a more complicated origin from a lower basic number? Close study of germ-cell formation in the apples and pears and medlars has shown (Darlington and Moffett, 1930, Moffet, 1931¹) that 17 is not the primary number, but is really derived from an earlier set of seven, like that found in roses and strawberries. This earlier set at a remote period was doubled in part and triplicated in the other part. If the earlier set of 7 was *ABCDEFG*, then the new set of 17 is *AAA, BBB, CCC, DD, EE, FF, GG*. It is *unbalanced* relative to the old set of seven, and it may be that the apple group owes its special characteristics, more particularly its fruits, to this change in balance. The relationship of the new type to the old may be represented diagrammatically as follows:—

¹ *J. Genet.*, 22, 129-63; *J. Pomology*, 10.

Ancestral Diploid

Set ($2x = 14$). $A A$ $B B$ $C C$ $D D$ $E E$ $F F$ $G G$ *Pyrus* DiploidSet ($2x = 34$). $A_1 A_1 A_2 A_2 A_3 A_3$ $B_1 B_1 B_2 B_2 B_3 B_3$ $C_1 C_1 C_2 C_2 C_3 C_3$ $D_1 D_1 D_2 D_2$ $E_1 E_1 E_2 E_2$ $F_1 F_1 F_2 F_2$ $G_1 G_1 G_2 G_2$

The result of this polyploidy is to give the apple the complexity of inheritance characteristic of polyploids, although the change took place so long ago that the apples have almost ceased to show any of the ordinary symptoms of polyploidy that have been described. With the polyploid constitution is associated behaviour of another kind—namely, compatibility in crossing. In diploids like the sweet cherry, incompatibility is often absolute in all varieties. And since new varieties of fruits nearly always arise as natural seedlings of old varieties of which there are a relatively small number scattered by vegetative propagation over the whole world, varieties of each species of cultivated fruit come to be a closely related family with groups of incompatible varieties. The pollen will never grow on the stigmas of a tree of the same variety, or any of the group. This is because a diploid with self-sterility factors cannot produce pollen sufficiently unlike itself to grow on itself. A related polyploid, owing to its greater chance of segregation, usually can. Plums and apples are therefore very often partially incompatible, giving moderate results on self-pollination (Crane and Lawrence, 1930¹). Nor does it do the polyploid so much harm to be selfed. Its self-fertilised progeny are still hybrid, and therefore need not lose vigour. In fact, there is no point in a polyploid being self-sterile.

¹ *Loc. cit.*

Another species which probably arose as an unbalanced polyploid and owes its special qualities to its new balance is *Dahlia Merckii* (Lawrence, 1929¹). This species differs from other dahlias in having thirty-six chromosomes instead of thirty-two or sixty-four. It is not in the eight-series, but has two extra pairs of chromosomes. It differs in form from all the other *Dahlia* species with multiples of eight by having fertile ray florets. It is another case of unbalance being a good balance.

¹ *J. Genet.*, 21, 125-59.

CHAPTER XVII

CONCLUSION

WE have attempted to find, for the guidance of the plant-breeder, the materials that transmit the hereditary qualities of the plant from one generation to the next; we have concluded that these materials lie in the chromosomes. Study of the behaviour of the chromosomes has shown how their constancy is preserved and how they vary. Particularly we see that in their reduction the chromosomes provide the mechanism of Mendelian segregation and at fertilisation the mechanism of Mendelian recombination. But in the various irregularities of their behaviour are to be seen the means by which types of inheritance can be developed much more complicated than any expressed in the simple Mendelian scheme, although they actually arise out of the same mechanism. Among these are the examples of true-breeding hybrids, such as the ring-forming evening primrose and the hexaploid bread wheat.

We also know now how sports arise from the presence of an extra chromosome and how the ever-sporting habit may be preserved by the loss of a piece of chromosome.

We can see how many important improvements in plants were brought about by polyploids. We know how such plant breeders as Thomas Laxton and Thomas Andrew Knight got the results they did, although working relatively in the dark. And we can therefore

imitate them in other fields which appear, in the light of a knowledge of the chromosome numbers, as promising as those they worked in. The occasional seedlings of sterile diploids can be raised in order to obtain fertile polyploids. Where a sterile hybrid is no disadvantage diploids can be crossed with polyploids.

We can see, moreover, that chromosome studies are particularly instructive in relation to fertility. Generational sterility is merely a symptom of segregation. It is due to the pairing and separating of chromosomes that are not sufficiently like one another (as in the diploid hybrid *Primula kewensis*), or to a less extent to chromosomes that are like one another pairing and failing to separate (as in tetraploid tomatoes). Further, there are many plants that are sterile, not on account of any hybridity in the ordinary sense, but simply because one of their parental germ-cells had two sets of chromosomes instead of one, so that they have an odd set which cannot pair normally at reduction. The degree of sterility to be expected in a plant can therefore be calculated to some extent from the pairing of its chromosomes and the pairing can be predicted from a knowledge of the parents' chromosomes. The plant-breeder therefore is in a position to decide before making a cross whether the results are likely to be fertile or sterile, and this is of great importance in the work of raising new economic plants.

Finally, we can understand a great deal more of the nature of species, a knowledge of which is as important to the plant-breeder, from one point of view, as it is to the systematist, from another. A study of the chromosomes shows at once that there are some species which are homozygous, uniform and true-breeding. These are the simple-pairing diploids. There are others, equally

true-breeding and uniform, which are of hybrid origin and have certain properties, more or less clearly shown, of hybrids. These are the ring-forming diploids and and hybrid polyploids. There are others again that contain several inter-sterile groups owing to polyploidy having arisen within them without hybridisation. And finally there are some that are seed-sterile hybrids maintaining themselves as uniform types by vegetative means such as bulb formation, apomixis, and so on. Cytological examination at once shows which of these groups a species falls in, and is a necessary preliminary to any systematic breeding work.

While chromosome studies therefore do not give the plant-breeder any greater control over his material, they enable him to direct his efforts into the right channels for obtaining and preserving the results likely to prove most profitable to him.

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¹ "Hawkweed" is used as the English equivalent of both *Crepis* and *Hieracium*.

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